MRes Thesis

The effect of artificial lighting on bats in Britain

Submitted by James Baker, to the University of Exeter as a thesis for the degree of Masters by Research in Biosciences, July 2016.

Summary

Artificial light pollution is increasing on a global scale at an annual rate of 6 per cent. Recent advances in artificial lighting technology are being developed at a faster rate than the ongoing replacement of conventional street lighting. This new technology is consumer driven for a broad band light spectrum, suitable for human vision, but little research has been conducted on its ecological impacts. Although it is known that light pollution can have major adverse affects on a wide array of species and ecological systems, research into the extent of these impacts is in its infancy. The most likely species to be adversely affected are those adapted to dark environments. Due to this, the focus of this thesis is on bats, a common nocturnal taxa in the UK, and the affects of artificial lighting on contrasting species within the taxa.

In this thesis, two approaches were taken; a large scale observational landscape investigation of the impacts of artificial lights (street lights) under current environmental conditions; and a small scale experimental investigation of the responses of bats to three lighting treatments: dark, UV-LED lighting, and filtered UV-LED lighting. In the former investigation, the focus is on a generalist species; *Pipistrellus pipistrellus* and a specialist genera; *Rhinolophus*. In both investigations the activity of *P. pipistrellus,* the most common bat in the UK, did not differ significantly at dark compared to artificially light locations. However, in the landscape study, the rate of foraging was 35% higher in dark locations (0.03 passes per detector night ± SE 1.17) compared to at street lit locations (0.02 ± SE 1.29; P = 0.027). In contrast, the activity of *Rhinolophus* spp. was 79% higher at dark locations (0.21 ± SE 1.00) compared to at street lit locations (0.04 ± SE 1.00, P = 0.052). No significant effects were found in the experimental study, possibly due to the high

variability of bat activity, insufficient replicates and insufficient differences between the light types.

The landscape study confirms that increased artificial lighting will have adverse effects on *Rhinolophus* spp., limiting the available habitat in the landscape for commuting and foraging. In contrast, *P. pipistrellus* activity was not affected by artificial lighting. However, reduced foraging was found in these locations, possibly due to altered insect composition at artificially lit locations, which may have negative indirect affects for this species. These results highlight the wider importance for all species of the ecological impacts of artificial lighting and contribute to the growing body of research in this area which discourages the continued trend for illuminating naturally dark environments.

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Acknowledgements

Firstly, I would like to thank my supervisors Prof. Fiona Mathews and Dr Henry Schofield for their support and advice. I would like to thank Julie Day, Dr Suzanne Richardson and Dr. Paul Lintott for their advice on statists and comments on the thesis. The research was funded by the Department for Environment, Food and Rural Affairs and the Vincent Wildlife Trust. I would like to thank Colin Morris for helping with access to the Vincent Wildlife Trust Reserves and landowners who made the research possible. I am grateful for the hard work by my field assistants: Dr Johanna Rabineau and Adrian Bailey.

Chapter one:

1. Introduction

1.1. Day and night, light and dark

A very diverse set of strategies for life on Earth have evolved, largely due to the uniquely tilted axis, rotation, and yearly orbit it takes around the sun. North and south of the equator distinct seasons are present throughout the year, and away from the poles the daily rotation creates light and dark over a 24-hour period. The resulting fluctuations in ambient light (solar, lunar and celestial) have been consistent for extremely long periods of geological time and have resulted in nearly all organisms evolving in parallel with these repeated cycles (Gaston et al., 2013). There is a significant variation in mammalian activity periods and visual adaptations vary accordingly across taxa (Walls, 1942). Humans are an example of a species which have adapted to be active during daylight hours (diurnal). Around 30% of all vertebrates and more than 60% of all invertebrates world-wide are nocturnal (Hölker, et al., 2010), and for these animals their night time niche has been promoted by highly developed senses, often including specially adapted eyesight. The main driver for these differing life strategy adaptations is widely accepted to be due to predator avoidance or predator adaptation (Lockard and Owings, 1974; Usman et al.,1980; Clarke, 1983; Price et al., 1984; Watanuki, 1986; Alkon and Saltz, 1988; Martin, 1990; Kotler et al., 1991). Most organisms, humans included, have evolved circadian clocks controlled by natural day and night cycles which influence metabolism, growth and behaviour (Dunlap, 1999). Humans have relatively recently separated from a true diurnal life strategy through the use of artificial lighting. Indeed, if human vision was not so acutely designed for diurnal activity, there would be no need for artificial lighting. The human condition drives us to be as 'productive' with our time as possible. Artificial light has enabled us to; work longer, increase social activities and sports as well as increase safety, reduce crime (or fear of crime), give us a sense of

place and provide aesthetics to our buildings and infrastructure. A combination of these things has created 'light pollution', a commonly used term, widely understood to describe the upward glare that obscures the view of the night sky. Ecological light pollution is suggested by Longcore and Rich (2004) as a more descriptive term which encompasses the following sources; illuminated buildings and towers, streetlights, vehicle lights, security lights, fishing boats, flares on off-shore oil platforms and more besides, all of which contribute to increased light pollution, including sky glow. This more defined term, ecological light pollution, describes the influence over the natural light regimes within terrestrial and aquatic ecosystems. Dark landscapes have been illuminated by artificial lighting for over a century, spreading with increasing urbanization and economic development. The amount of artificial lighting on a global scale has increased concurrently with a rising human population, increasing at an annual rate of 6 per cent (Hölker et al., 2010). Data collected in 2015 by the National Oceanographic and Atmospheric Administration (NOAA) shows that only 22% of England's skies are free from light pollution. Fifty three percent of dark skies in England are above National Parks and Areas of Outstanding Natural Beauty (LUC 2016).

Animals and plants have had to adapt to or suffer the consequences of light pollution only over a very recent evolutionary time period. The fundamental problem with light pollution is that the light levels produced at localized sources are of a similar intensity for certain wavelengths to natural levels in daylight (Hollwich, 2012). There are many examples where organisms have been shown to be sensitive to extremely low levels of light at night, comparable to anthropogenic light pollution (Kelber and Roth, 2006; Bachleitner et al., 2007; Evans et al., 2007; Frank et al., 2010). Artificial lighting on a grand scale, has resulted in the loss of twilight cues, for many organisms, of the

daily, seasonal and lunar cycles in light intensity. A normal, unaltered lunar cycle can be one of the most important signals that wildlife has adapted to recognize and respond to.

Among marine animals, Bentley et al., (1999) conclude that an interaction between solar and lunar signals is widespread in the timing of reproduction. An example of this is plankton rising and falling within completely dark oceans in response to changes in light levels that are not perceptible to humans. Light is the fundamental controlling factor in diel vertical migration (DVM) of zooplankton, with either the nocturnal or twilight pattern most commonly observed. This rising and falling of zooplankton within large bodies of water enables feeding in warmer richer water closer to the surface and protection from filter feeders at colder depths. A study of zooplankton at a lake in Norfolk County, MA showed that artificial light at the site had the same effect as a full moon on DVM (Moore et al., 2001). While ecological light pollution may not be considered by many as threatening to ecosystems to the same extent as habitat loss, anthropogenic disturbance caused by artificial night lighting has been shown to influence foraging behaviour (Kuijper et al., 2008; Stone et al., 2009; Stone et al., 2012), reproduction (Rand et al., 1997), growth and sexual maturation (Oppedal et al., 1997) and communication (Longcore and Rich, 2004), over an extensive range of taxa. In Kolbeterberg, Vienna, (Kempenaers et al., 2010) monitored blue tit breeding between 1998 and 2004 in artificially light territories and naturally light territories. They found that males sang mating calls earlier in the artificially light territories resulting in a breaking of the link between male quality and dawn song leading to maladaptive mate choice. Females were also found to lay eggs earlier, potentially leading to a mismatch between the time of food demand and peak food availability.

In some environments the presence of artificial lighting can have a seemingly positive impact on some species. Urbanization may favour some species which succeed in human-altered conditions because they perform well in heterogeneous landscapes (Magle et al., 2012), benefit from the increased temperatures associated with urban areas (Pickett et al., 2001) or use the latter to shelter from large predators (Baker and Harris, 2007). Lighting can improve some species' hunting strategies by exposing prey more readily and or rendering prey unable to comprehend their environment effectively. Examples include amphibians being blinded for lengthy periods (Cornell and Hailman, 1984; Donner and Reuter, 1962) and some moth species failing to respond naturally to the echolocation calls of bats (see below). There are further examples of artificial lighting both intentionally and unintentionally benefiting some animals. Lighting has been used to draw fish to alternative routes away from dams and power plants (Haymes et al., 1984) and in other cases to attract larval fish to reefs (Munday et al., 1998). Land based examples include diverting mammals from road crossings using reflected light and progressively encouraging bats out from tunnels to safety before the arrival of an oncoming train (G. Billington, 2013, personal communication). It should be noted that while we may consider these actions as benefiting wildlife, they are only being used to mitigate the problems created by anthropogenic affects in the first instance.

1.2. Insects and light

Artificial light has the potential to affect insects in many ways, including disrupting their foraging, dispersal, breeding, interspecific interactions (Frank, 2006; Altermatt et al., 2009) and predation (Svensson and Rydell, 1998). Insects of the orders; Coleoptera (beetles), Diptera (flies), Hemiptera (bugs), Hymenoptera (sawflies,

wasps, bees and ants), Lepidoptera (moths and butterflies), Neuroptera (lacewings, antlions and mantidflies), Orthoptera (grasshoppers and crickets) and Trichoptera (caddisflies) are well documented to be affected by artificial light. Insect behaviours have evolved in the absence of lighting for millions of years, so it is understandable that their actions are so influenced and unnatural in the presence of artificial lighting. Flight-to-light has been attributed to insects misinterpreting light sources for natural light used as orientation cues, such as the moon and possibly other celestial objects. Disruption by the overwhelming brightness of artificial light to insect vision may also be a significant factor causing a dazzling effect (Robinson and Robinson, 1950), especially the closer an individual is to the source. Other theories extend to a temporary blinding effect caused by movement of screening pigment in the eye (Hamdorf and Högland, 1981) or the perception of light as an open space (Altermatt et al. 2009).

Moths are able to detect and respond to ultra violet (UV) light reflected from the moon, and use the azimuth (angle of the sun) for navigation (Sotthibandhu and Baker, 1979). The fact that many moth species are brightly coloured and patterned (when they occupy much of their time flying at night) suggests that colour, and hence light, is important to their ecological functions. It is the intensity of artificial lighting being so high that disrupts these normal functions, and lighting containing UV wavelengths prevent normal flight and navigation. Recent studies have shown that moths are more attracted to lamp types containing shorter wavelengths (F van Langevelde et al., 2011), finding higher species richness and abundances than at lamps with higher wavelengths. White type lights are characterized by short wavelength light and yellowish type lights characterized by long wavelength light. The UV element of the light is a significant factor, with a higher UV content being

more attractive to insects (Eisenbeis, 2006; F van Langevelde et al. 2011; Barghini and Medeiros, 2012). For moths that remain at a safe distance, artificial lighting may improve vision; the UV photons emitted by such lighting will accentuate UV markers on flowers (Barth, 1985) enabling easier navigation to nectar. In contrast, low pressure sodium vapour light does not contain UV and so flower markers are concealed.

A moth that is fortunate enough to escape the attraction to artificial light, may still suffer the consequences of exposure as it flies to a darker environment. A continuing blinding effect may extend to 30 minutes after a one second exposure to light for the *Noctuidae* species *Cerapteryx graminis*, as the reactive pigments and cells in the eye normalize to dark conditions (Bernhard and Ottoson, 1960). It has also been shown that light exposure can influence the reaction of male moths to female pheromone production. Male moths exposed to green, red and white light treatments showed less attraction to pheromones than at dark treatments and the activity of females was shown to be reduced in the light treatments (Geffen et al. 2015).

Tympanate moths have special auditory organs ("*tympani*") which facilitate detection of the ultrasounds emitted by bats, so that an evasive response can be made to avoid capture. They can alter their trajectories in several ways; falling as if they were inanimate objects, stopping flight temporarily or even emitting sounds that deter attack by jamming the echolocation of the pursuing bat. It has been observed that these moths, when flying around artificial light sources, do not implement defensive strategies in the presence of bats (Acharya and Fenton, 1999) and it has been demonstrated experimentally that certain moths, when exposed to the light of mercury vapour lamps, adopt defensive behaviour much less frequently than when

they are not exposed to and under the influence of this type of light (Svensson and Rydell, 1998). It has been estimated that one third of moths attracted to artificial lighting do not survive (Eisenbeis 2006). The risk environment for insects flying around lights can be increased due to the effects of; exhaustion, burning, dehydration and predation. Repeated impacts can damage wings and cause scale loss. The heat contained within the lamp housing and its surface can incinerate moths on contact. Overheating and desiccation can occur in close proximity to lamps, resembling the effect of radiation from the sun in the daytime, for which nocturnal moths have evolved to avoid, by being active at night.

The implications of this attraction to light by insects also reduces their time, and hence efficiency, at doing whatever they would or should be doing if it were not for the presence of artificial light, for example foraging or mating. Significant losses to populations can occur for species which are migrating or mating. Natural courses of migratory movement can be altered and many individuals can become trapped by the attraction to artificial lighting. Species which naturally reproduce in riparian habitats have been recorded laying their eggs on the road surface beneath street lighting, after being drawn away from water bodies. With the life cycle of insects, such as the mayfly, only extending a few hours out of water, this disruption to behaviour can be catastrophic to local populations; an estimated 1.5 million individuals were found dead after helplessly laying their eggs on the illuminated road surface of a bridge (Tobias, 1996).

Insects are critically important to pollination and the complex food web, with such obvious impacts upon insect behaviour and breeding, it follows that artificial lighting, particularly that of a higher UV content, will have higher trophic level effects.

1.3. Bats

The Chiroptera order make up about one-quarter of all mammal species and 977 species have been classified (Corbet and Harris, 1991) into two suborders, namely, Megachiroptera and Microchiroptera. The Megachiroptera are often referred to as the Old World fruit bats and are large, non carnivorous; feeding on fruits, flowers and nectar. This non-echolocating suborder consist of 162 species which are tropical or subtropical. The Microchiroptera are smaller (typically 5-20g) with 815 species that predominantly feed on insects and use ultrasonic echolocation. The 17 families of Microchiroptera are found across the world excluding the polar regions. Diversity amongst this order is highest throughout the tropical regions.

The difference in size between the two sub orders is directly related to their respective diet choices. The Megachiroptera bats can be larger with greater body mass since the food they seek is stationary and high levels of manoeuvrability in flight are not required. The size and mass of insectivorous bats is limited by their requirement to be highly manoeuvrable in the pursuit of small, flying prey. However, although the requirement to be small is clear, there is still a high degree of variation of size within this sub order, as well as, differences in wing morphology and echolocation use. Wing morphology and echolocation type are closely related. Echolocation call structure; frequency, intensity, duration and pulse interval duration, are all determined by the challenges faced by the bat to perceive its natural environment (Jones and Holderied, 2007), and as such, each species' has evolved different call design to manage their environment and prey items. In general, higher frequency echolocation is used by the more manoeuvrable species that have broad wing shaping and are slower flying. These high frequency calls attenuate in air more quickly and this limits the effective range of detection of objects and prey (Griffin,

1971; Lawrence and Simmons, 1982). Thus, information about the environment must be updated more frequently by bats using higher frequencies and so the time between echolocation calls is minimized such that continual imaging of the environment is achieved. This combination of wing morphology and call type enable a high degree of manoeuvrability in clutter based environments. Bats which use lower echolocation frequencies are more suited to edge and open habitats, are less manoeuvrable but faster flying. Lower echolocation frequencies travel further and so environmental imaging extends to a greater range. Because low echolocation frequency calls travel further, allowing for the speed of sound to rebound back from objects, time between echolocations (inter pulse interval) is increased so as not to obliterate the echo with a subsequent call. Thus, less detail about the environment is gained and less frequently, resulting in open habitat preferences. Frequency bandwidth is another factor of call structure which informs us about the environmental preferences for different species of bat. Species that emit calls with broad band-widths (large frequency range) are most successful hunting in clutter environments (Siemers and Schnitzler, 2004). For example, *Myotis nattereri* can frequency modulate its calls from 135 kHz to 16 kHz (Russ, 2012). Calls of this nature reflect off many surfaces, including prey and vegetation simultaneously, enabling environmental imaging for discrimination between prey and clutter (Siemers and Schnitzler, 2004). Although clutter species specialize in this form of broadband echolocation, other species more associated with lower more constant frequency echolocations display a relatively high degree of plasticity and can incorporate more frequency modulation to their call structure and reduced inter pulse intervals as required, such as when closing in on a prey item or in a more cluttered environment.

Insectivorous bats of the temperate latitudes usually time their flights to coincide with darkness (Erkert, 1982). As alluded to earlier, this is largely a predator aversion strategy. The faster flying species tend to emerge from their roosts shortly after sunset, whereas the slower flying species delay emergence, waiting for a darker environment (predator aversion). Speakman (1991) considers competition with insectivorous birds as a reason for bats choosing to forage at night but concludes that bats in Britain do not fly more frequently during the day due to the risk of predation. This nocturnal strategy results in bats being potentially very sensitive to effects of artificial lighting on their insect prey and their interpretation of predator risk.

A large proportion of the time spent by an insectivorous bat flying at night is dedicated to foraging; the remaining time is spent searching for a mate, a roost or drinking water. Artificial lighting can therefore affect any of these behaviours. Many studies have been conducted observing bats foraging around streetlights and artificial lighting as a method to understand their echolocation and hunting methods. Advances in understanding the behaviour and flight characteristics have been made in this way over the decades; (Webster and Griffin, 1961) documented observations of bats that caught insects around an illuminated porch screen, which enabled them to study hunting techniques and subsequently wing morphology. In more recent decades, artificial lighting has been used as a study site for bat echolocation and hunting strategy research (Fenton and Morris, 1976; Shields and Bildstein, 1979; Belwood and Fullard, 1984, Schnitzler, 1987). The effects and relative merits for bats choosing to feed at a point source of artificial lighting were also beginning to be considered, rather than just using a light source as a mode to study bat morphology Fenton et. al. (1983).

Throughout these studies, certain morphological characteristics that enable feeding around a point source of light have become apparent. Only certain bat species actively and repeatedly forage around artificial light sources (Rydell, 1992). This is thought to be governed by risk tolerance, evolutionary strategies to avoid predation (Speakman, 1991), speed of flight and echolocation call type (Rydell, 1992). Species diversity within the Chiroptera order has resulted in various strategies being implemented (or *vice versa*), broadly based on speed of flight, manoeuvrability and echolocation type. Bats frequently observed feeding at streetlights are of the fast flying type described above. The two generically described types (fast and slow) can also be categorized in terms of their preference of foraging habitat, as well as their tolerance to light. In general, slow, manoeuvrable species with high echolocation frequencies are specialists in cluttered environments and are often termed 'light shy'. The fast flying species, with lower echolocation frequencies, hunt in uncluttered environments (Neuweiler, 1989) and are often termed 'light tolerant' species. These differences are attributed to their ability to avoid predators. The light shy species most likely rely on complete evasion, hence their emergence strategy. The light tolerant species on the other hand, are fast enough to stand a chance of evading a predator such as a hawk. Of course, within these two extremes of category type lies a continuum of variation of flight and echolocation attributes.

These differences are also reflected in the roost emergence behaviour adopted by the two types. The light shy species of bat are characterized by delayed evening emergence which is also extended in time, compared to the light tolerant species which emerge earlier and over a shorter time span (Jones and Rydell, 1994; personal observation).

Foraging around streetlights can be a beneficial hunting strategy for light tolerant bats. In a study at Kootenay National Park, Fenton et al. (1983) claimed that at the time of their study the species *Lasiurus cinereus* would not be present without the presence of streetlights drawing in prolonged concentrations of insects. European bats which are often observed foraging around street lights include *Eptesicus*, *Pipistrellus*, *Nyctalus* and *Vespertilio* spp. (Rydell, 1992). These species are, as discussed above, adapted to open flight foraging and are less wary of potential predation. The attraction to street lighting as a foraging site is as a result of improved efficiency prospects which are increased in rural areas where insect fauna is in close proximity. In more densely lit cities and large towns the draw to street lighting by insects may not be so great due to lower abundance (Taylor et al., 1978; Frankie and Ehler, 1978) and hence, fewer bats are found and likely to survive there (Geggie and Fenton, 1985; Kurta and Teramino, 1992). Within the UK, the *Pipistrellus* spp. are the most reported species found to exploit insects at streetlights. *Pipistrellus pipistrellus* were the only species found foraging around streetlights at study sites in the south of England (Blake et al., 1994).

1.4. Risk for bats at streetlights

There are related risks for bats adopting a hunting strategy around streetlights. Since bats vision is adapted for low light levels, it is likely that foraging around artificial light reduces their perception of predator risk. Repeated use of streetlights for foraging increases the risk of being hit by vehicles in certain circumstances and can expose their presence to nocturnal predators such as domestic cats and owls. Diurnal avian predators and opportunists such as hawks, crows and gulls may also respond to bat activity (Gillette and Kimbrough, 1970). These predators and opportunists can

quickly learn to repeatedly hunt at an area which has a concentration of prey (bats) just as bats do with insects. The light shy bat species appear to consider these risks too great or are simply too conditioned by adaptation to darkness and clutter based foraging to hunt around streetlights.

1.5. Bat Vision

The physiology of the eye has been of interest to scientists in trying to explain the differences in tolerance to light between bat species. How different mammals respond to light depends on the design of the eye and its components. The pupil, lens and type of photosensitive cells in the retina, determine sensitivity to light intensity and wavelength.

Vertebrates have specialized light receptor structures identified as either rods or cones which layer the retina in the back of the eye (Malmström and Kröger, 2006). Rod photoreceptors are narrow and cylindrical in shape, are highly sensitive to light and used for night vision. Cone photoreceptors are thicker, less cylindrical and less sensitive to light and used for daylight and colour vision. In general, nocturnal mammals have large pupils to receive maximum light, large lenses to reduce spherical aberration and retinas dominated by rod cells (Walls, 1942). It takes only a few photons of light to stimulate a rod cell. Having a large proportion of rod cells results in a high sensitivity to light but low acuity, meaning detail is poorly rendered. In contrast, it takes a large number of photons to stimulate a cone cell, which means that an eye with a high proportion of cone cells is very capable of high detail vision in highly illuminated conditions. It has long been thought that bats have lost the use of much of their vision following an evolutionary pathway of increased hearing sensitivity used in conjunction with echolocation (Speakman, 2001; Zhao et al.,

2009). This is also supported by observing the relative size of the eye in relation to the size of the skull. Many nocturnal mammal species have developed very large eyes to gather as much light as possible. A cursory glance at the head of various nocturnal mammals (e.g. Tarsier (family Tarsiidae), Slow loris (Lorisidae), Kinkajou (Procyonidae), Pygmy possum (Burramyidae)), in comparison to insectivorous bats, reveals that vision is a much relied upon sense. Insectivorous (echolocating) bats have very small eyes in relation to their skull size compared to other nocturnal mammals, including Old World fruit bats (Zhao et al., 2009) suggesting that vision comes secondary to echolocation and auditory senses. However, experimental and observation evidence suggest that echolocating bats make use of vision and in some cases rely on vision in preference to auditory/echolocation cues for; long-distance orientation (Griffin, 1970), detection of landmarks (Davis, 1966), avoiding obstacles (Bradbury and Nottebohm, 1969) and prey detection (Bell, 1985; Bell and Fenton, 1986; Eklöf and Jones, 2003). The perception of light must also be important to bats in terms of their ability to know when to emerge from and return to a roost. Several bat species are known to undertake test flights within the roost before they exit in a procedure that is called light sampling (Erkert, 1982; Fure, 2006), whereby, individuals from the colony fly from dark areas within the roost to lighter areas near the entrance. In some cases, this can extend to short excursions from the exit before returning inside as observed at many *Rhinolophus hipposideros* roosts. Some form of communication within the colony may occur during this procedure. Based on personal experiences of capturing bats in hand nets at the roost entrance, it has proven effective to let the first few bats depart before commencing capture. If one of the light sampling bats detects the net, then the colony delays emergence and one ends up waiting longer than normal for the emergence of the colony to commence.

These test flights are thought to be a method of setting a biological clock, as well as, determining predation risk related to light levels. It has also been observed that bats tend to swarm near the roost entrance before returning at dawn, also thought to be related to resetting the biological clock (H Schofield 2014, personal communication).

Orientation cues can be obtained through the perception and interpretation of natural light. *Myotis myotis* bats were studied returning to roost after being captured, translocated and then released (Holland et al., 2010). The bats seemed to be using sunset cues to calibrate an internal 'magnetic compass' to orientate themselves. This is a remarkable explanation given that this species normally delays activity until well after sunset when only a faint glow from the sun is present. Discoveries of this nature have compounded hypotheses' that bats and other mammals can use natural light (polarised) to orientate themselves in much the same way as birds. Since birds are largely active during daylight hours, they are exposed to and make calibrations from solar polarization. Bats that emerge and fly while the sun's rays are still in the sky may also use this solar polarzation as described by Holland et al. (2010). Lunar reflected light entering the earth's atmosphere is also polarized and to the same linear degree as solar light (Gál et al., 2001); however, the intensity of lunar light is many orders of magnitude dimmer than sunlight, making perception, and hence orientation, far more difficult (Warrant, 2004). However, even on new moon nights, when light is reflected from the thinnest of crescents, dung beetles (Coleoptera: Scarabaeidae) where shown to be able to orientate using lunar polarization (Dacke et al., 2003; 2011). While full understanding of orientation methods used by animals perceiving lunar polarization is incomplete, it might be predicted that artificial light pollution will diminish the degree to which polarized light can be used as a navigation

aid. Typical street lighting is not polarized but across urban areas the scattering of light in the atmosphere (Kerola, 2006), and from natural and artificial surfaces (Koennen, 1985) (such as flat water, tarmac and windows) can create polarized light, and sky glow on a large scale will likely pollute lunar polarization (Kyba et al., 2011).

Different types of photoreceptors occur in the eye. Cone cells contain pigment that is most sensitive to light at wavelengths less than 400nm (Hunt et al., 2001). The UV portion of the light spectrum covers wavelengths between 100 and 400nm including the UV-A, UV-B and UV-C portions. Rod cells present in the eye are the photoreceptors that provide scotopic vision (low light conditions where colour vision is absent). It has been believed for some time that the retina of microchiropteran bats contain only rod cells. The cornea and lens in humans absorb damaging UV-A and most UV-B radiation, preventing these reactive wavelengths from hitting the retina (Carvalho et al., 2010). In a study of four species of bat to investigate UV light tolerance (Fujun et al., 2012), it was found that the bats of a Hipposideridae-Rhinolophidae linage did not respond to a source of UV light, therefore had no capacity for UV vision. This suggests that cone cells are not present or active in the eye in this family of bat. In contrast, they found that bats studied of the Vespertilionidae linage did respond to UV light, suggesting cone cells are present and could be used for orientation and/or hunting. Of the two species of Old World fruit bats studied, they found that the cave roosting species did not react to UV whereas the tree roosting species did, suggesting that UV light perception may be a determining factor for roosting ecology.

Several studies have suggested that microchiropteran vision is most effective in dim ambient light (i.e. dusk and dawn) compared to bright daylight (Bradbury and Nottebohm, 1969; Ellins and Masterson, 1974; Hope and Bhatnagar, 1979). The

evidence of the presence of cone photoreceptors in some bats indicates that vision in low to intermediate light levels (mesopic vision) is possible but is saturated at high levels encountered in daylight (Müller et al., 2009). It is also likely that damage to the eye may occur in the presence of UV light (natural or artificial sources) since the eyes of nocturnal bats have evolved for low light levels (low UV content) (Fure, 2006). The intensity of a light source shone on the exit of a *Pipistrellus pygmaeus* roost was found to have more of an effect on the emergence behaviour than the colour of the light source (Downs et al., 2003). In contrast, Laidlaw and Fenton (1971) illuminated maternity roosts of little brown bats (*Myotis lucifugus*) and big brown bats (*Eptesicus fuscus*) from the inside and found emergence in all cases was earlier, concluding that light within the roost would make it seem darker outside and that light was a cue for nightly departure. However, earlier departure could also be attributed to the bats wanting to get out into the darkness away from the bright lights. In any event, these examples provide further evidence that bright lighting (intensities much brighter than ambient levels at dusk), of different colours i.e. wavelengths, is detrimental to bat behaviour. Studies will probably continue to try and understand how reactive and sensitive the eyes of bats are to various portions of the light spectrum.

1.6. Natural Light affects behaviour

Bats have existed alongside insects, developing a complex predator-prey evolutionary arms race over a 65-million-year time span (Conner and Corcoran, 2012). The natural rhythms of light and dark, and the continuum between, have created over this extensive period of geological and evolutionary time period, entrained behaviours and responses in bats as well as all other mammals to

changing intensities and wavelengths during the course of the day, season and year. The free running period of activity, the activity cycle for an animal under constant light or darkness, ranges from 23 to 25 hours for most vertebrates, with extremes of 21 to 27 hours. Circadian rhythms are endogenous ('built-in', self-sustained) and are entrained to the local environment by external cues called zeitgebers, commonly the most important of which is daylight. The quantity and spectral makeup of light at dawn and dusk are significant factors in synchronizing the internal clocks of vertebrates (Foster, 1996). For these animals, the photoreceptors containing rods and cones, do not entrain the biological clock. In mammals, a photoreceptor system located in the retina is linked to the suprachiasmatic nuclei (SCN) in the brain via a different neural system to the rod and cone photoreceptor system (Foster and Provencio, 1998). Typically, light of higher quantity than that required to form a visual image is needed to shift the circadian rhythm and must be of a duration in the range of 30 seconds to 100 minutes. Thus, occurrences of natural phenomenon, such as lightning, are sufficiently bright enough but not extensive enough in time to cause a shift or resetting. In contrast, starlight and moon shine are extensive enough in time but not bright enough to cause a shift in most mammals. However, bats have been shown to exhibit entrainment at illuminances as low as 10^{-5} lx (several orders lower than moonlight) (Erkert, 2004). Contrasting results have been shown in studies where observations of bat activity have been made in relation to moonlight levels. Some studies have shown little adaptive behaviour in bright moonlight for insectivorous bats (Negraeff and Brigham, 1995; Hecker and Brigham, 1999), whereas, others have found significant reduction in activity and changes to foraging habitat preferences e.g. (Fenton et al. 1977). In studies of fruit bats, reduced activity was found on nights with high levels of moonlight (Morrison, 1978; Law, 1997;

Elangovan and Marimuthu, 2001). A similar trend was found in a study of the predatory greater false vampire bat *Megaderma lyra* (Subbaraj and Balasingh, 1996). These behaviours were largely attributed to reducing perceived risk of predation as outlined earlier. It is clear though, that different bat species have varying sensitivities to light and this is reflected in their different roosting choices, emergence times, flight characteristics and habitat preferences.

1.7. Artificial light affects behaviour

Artificial light sources contain wavelengths in the UV spectrum of varying intensity depending on lamp type. This raises the possibility that artificial lighting could be problematic for bats which can detect or use UV light for spatial or temporal cues, including interference with regulation processes controlled by the circadian rhythm. Artificial sources of UV may be confused with natural UV which could have numerous sensory effects. Knowledge of the function of biological clocks in different species, parameters of light characteristics (spectrum, intensity, length of exposure etc.) and the mechanisms with which organisms respond to light stimulus, is at present limited. Some experimental studies have shown that artificial light can impose unnatural behaviour on bats during night activity.

The number of bat passes of *Myotis lucifugus* was significantly reduced when a crossing point was artificially illuminated compared with when the lights were turned off, indicating reduced activity (McGuire and Fenton, 2010). *Rhinolophus hipposideros* showed a dramatic reduction in activity with the presence of artificial lighting (high-pressure sodium lamps). The roost emergence time was found to be delayed and the number of bat passes significantly reduced. Reduced activity was also recorded when monitoring activity along a hedge which was illuminated on the

other side, indicating that low levels of light have a negative effect (Stone et al., 2009). Individuals of *Myotis dasycneme* briefly modified their flight trajectories in reaction to being exposed to halogen lamps (Kuijper et al., 2008).

These studies show that artificial lights can act as barriers reducing habitat availability and potentially forcing bats to change their flight routes to alternative ones, with possible negative consequences. Alternative routes may be longer, requiring greater energetic costs and more hazardous; hostile conditions such as predators, reduced contact with suitable habitat and exposure to bad weather conditions. Delayed and extended roost emergence as a result of artificial lighting can also be energetically costly in terms of food resource availability, since insect activity is known to be highest in the period around sunset (Racey and Swift, 1985; Rydell et al., 1996). Bats delaying their emergence under the influence of artificial lighting will miss this peak in insect abundance. This can have increased consequences for lactating females; having higher energy requirements and females in late pregnancy; having higher wing loadings (Duvergé et al., 2000).

1.8. Roosting preferences

Bats choose to roost in sites that vary in size from species to species but most locations are characterised by a preference for darkness. Whether they are large roosts; caves, disused mines/tunnels, rooms/attics in buildings or small roosts; cavities or fissures in stone or trees, they offer varying degrees of protection from light. Tolerance to light within roosts has been known to occur where colonies remain faithful to a site and have adapted to a change in their environment. *Rhinolophus ferrumequinum* have shown a certain tolerance with respect to light levels recorded in their roosts and can be found in sites that are moderately lit, although most roosts

are particularly dark (C. Morris 2014, personal communication). It has been reported that breeding colonies of bats have abandoned roost sites where artificial light has been implemented in or close to the roost (Laidlaw and Fenton, 1971). Within a maternity colony of *Myotis velifer* located in a cave, disturbance to the bats was largely attributed to light intensity over other factors created by visitors (Mann et al., 2002).

As described earlier, roost emergence times and emergence duration vary between species, largely dependent on risk tolerance to predators. Artificial light near a roost exit can disrupt an individual bat's perception of ambient light levels and hence predation risks. For the species' which are known to undertake light sampling, this assessment of localized light levels (predation risk) can affect the whole colony since only a few individuals make the test flights before the colony emerges. This synchronized emergence based on test flights made by a few can delay the departure of the whole colony reducing prime foraging time.

Functional effects of artificial lighting have been studied at church roosts in Hungary (see Boldogh et al., 2007). Emergence times and duration of *Myotis emarginatus, M*. *oxygnathus and Rhinolophus ferrumequinum* were recorded in light and dark scenarios. *M*. *oxygnathus* were monitored emerging from one roost on two consecutive nights, consisting of a light treatment of one hour after dusk on the first night and no light on the next. Emergence rates were reduced on the first night while the lights were on, which subsequently increased when the lights were turned off. On the following non-illuminated night, the bats resumed to more normal emergence behaviour. *Rhinolophus ferrumequinum* were also residing within this roost and displayed similar behaviour; reduced rates of emergence from the roost whilst illuminated but returning to near normal emergence rates on subsequent non-

illuminated nights. Two *M*. *emarginatus* roosts were studied on the same night; one illuminated for approximately two and a half hours after dusk, the other non illuminated. The bats at the illuminated roost did not emerge at all until after the lights were turned off, while most of the bats at the non-illuminated roost had emerged within 30 minutes of dusk. This species did not return to normal emergence behaviour on subsequent non-illuminated nights as quickly as *M. oxygnathus* and *Rhinolophus ferrumequinum*. Indeed, roost abandonment was recorded at one of the roosts studied, after the local council installed lights which poured light through the main exit, completely illuminating the loft space. In such a case, where a colony abandons a roost completely, a compounding effect may result. Many species of bats exhibit a maternity site fidelity (Lewis, 1995), whereby the females return to their place of birth to give birth themselves. If their original roost has become unsuitable they may find it difficult, or possibly lack instinct, in finding an alternative.

Pup development of *M*. *emarginatus* and *M*. *oxygnathus* from these roosts was also studied showing significant differences in development between the illuminated and non-illuminated roosts. Both forearm length and body mass of the juveniles measured from the illuminated roosts were less, compared with juveniles measured from the non-illuminated roosts. Although exact birth dates were not known, well developed young were found at one of the undisturbed roosts while pregnant females were found at an illuminated roost, indicating delayed birth dates due to lighting.

A measure of body mass growth rate reflects environmental conditions more accurately than measuring forearm growth rate (Kunz and Robson, 1995). Hibernation success is largely dependent on body mass (fat reserves) obtained

during the summer months (Ransome, 1998). This is particularly significant when females delay parturition and have reduced feeding time at illuminated roosts.

1.9. Species most affected by artificial light

There are a range of morphological characteristics across species, which, ultimately determine each species' resilience to the dramatic human induced changes in the environment. Anthropogenic disturbance on the biotic and abiotic environment appears to have more of an impact on short, broad winged bat species which use higher frequency echolocation methods (Jones et al., 2003; Safi and Kerth, 2004). Environmental perturbation, including artificial lighting amongst other disturbances, is a key factor (detrimental) for many of the UK bat species.

Larger scale effects of artificial lighting have been considered; If individuals are feeding at point sources of light, what might be the affect of a large number of lights such as a village, town or even city? Researchers have started to investigate why and to what extent some species of bats are using streets lights to forage and whether this could be to the detriment of bat species which do not favour this method of foraging (Arlettaz et al., 1999). The cumulative draw of bats to many streetlights has not been studied to such a degree as the study of the draw by a few lights. If we consider two insectivorous species of bat which have similar diets and one of these species does not habituate to foraging around artificial light then the possibility arises that, given insects are more likely to accumulate at artificial light sources, the 'light shy' bat species could be losing out to a shift in insect abundance from the naturally dark to artificially lit areas. Regardless of any food source shift patterns that may be occurring, the species that could be suffering most from artificial lighting are likely to

be already threatened taxa due to a combination of anthropogenic changes which have preceded light pollution.

1.10. Objectives of research

Increasing light and effects on wildlife is relatively new phenomenon and as such little research has been done. The effects are anticipated to be greatest for nocturnal species such as bats. Specifically This thesis aims to assess the impact of artificial lighting on two contrasting species of bat at a landscape scale. This is investigated in two ways;

1. Is activity for *Rhinolophus hipposideros* and *Pipistrellus pipistrellus* altered at artificially lit locations compared to dark locations across the wider landscape in an observational experiment?
2. Does bat activity along commuting routes alter with installed artificial lighting and is this influenced by changes to the intensity of the ultra violet light component?

Chapter two

2. The effect of artificial lighting on bats: a landscape study

2.1. Summary

Artificial light pollution is increasing as the human population expands and is a major threat to many species, particularly those adapted to nocturnal strategies. To assess this impact, the effects of artificial lighting on bats was studied at a landscape scale. Bat activity was monitored at dark and artificially light locations using acoustic detectors within a 2km radius of eight *Rhinolophus hipposideros* roosts in the South West of England. Activity of *P. pipistrellus,* the most common bat in the UK, did not differ significantly at dark compared to artificially light locations. However, the rate of foraging was 35% higher in dark locations (0.03 passes per detector night ± SE 1.17) compared to at street lit locations (0.02 ± SE 1.29; $P = 0.027$). In contrast, activity of *Rhinolophus* spp. was 79% higher at dark locations (0.21 ± SE 1.00) compared to at street lit locations (0.04 ± SE 1.00, $P = 0.052$). These results confirm that increased artificial lighting will have adverse effects on *Rhinolophus* spp., limiting the available habitat in the landscape for commuting and foraging, since they avoid artificially light environments. In contrast, *P. pipistrellus* activity was not affected by artificial lighting. However, reduced foraging was found in these locations, possibly due to altered insect composition at artificially lit locations, which may have negative indirect affects for this species. These results highlight the importance of considering the ecological impacts of artificial lighting for infrastructure and housing developments and limiting the expansion of artificial lighting on a landscape scale.

2.2. Introduction

Large areas of the world are artificially illuminated at night (Cinzano et al., 2001). As the human population continues to increase, concurrently light pollution is increasing, estimated at a rate of 6% per annum (Hölker et al., 2010). As a result, animals and plants have had to adapt to or suffer the consequences of light pollution over a relatively short evolutionary time period. Some species have taken advantage of artificial lighting, for example, some nocturnal species feed in areas of concentrated prey around lit areas (Blake et al., 1994; Jung and Kalko, 2010) and some diurnal and crepuscular species can extend their hours of activity (Negro et al.,2000). However, for many species, behaviours including communication, foraging and reproduction, are negatively influenced by artificial lighting (for overview see Rich and Longcore, 2006) and is of particular concern for nocturnal animals.

Bats, are the second largest order of mammals, and those which are found within the temperate zone are largely nocturnal (Speakman, 1991). Nocturnal bats are acutely exposed to the influence rendered by artificial lighting, including at or near roosts and within the wider landscape where they forage. Previous studies which have investigated the effects of artificial lighting on bats have largely been experimental studies conducted within or close to maternity roosts (Downs et al., 2003, Stone et al. 2009, Zagmajster 2014). These studies have highlighted the potential problems for bats of artificial light close to a roost, including; delayed emergence, reduced activity and flight path aversion in response to experimental lighting. While these studies have provided evidence for light aversion for some species, they have lacked in scale and have not assessed the affect of artificial light across the wider landscape. In a few studies, artificial lighting has been found to benefit some species, such as *Pipistrellus pygmaeus*, where increased foraging

opportunities have been recorded (e.g. Bartonička et al., 2008). For this species, Downs *et al.* (2003), found that artificial lighting delayed roost emergence. Thus, for some species, a cost-benefit analysis of the effects of artificial lighting can be complex (Hale et al., 2015).

Most research on the effects of artificial lighting on bats to date, finds that relatively fast flying generalists, such as *Pipistrellus* species, are light-tolerant (Barak and Yom-Tov, 1989; Haffner and Stutz, 1985; Mathews et al., 2015; Russo and Jones, 1999; J Rydell, 1992; Speakman, 1991). In contrast, slower flying, specialists, such as *Rhinolophus* species, are light-shy (Stone et al., 2009; 2012; Zagmajster, 2014) and rarely recorded in artificially lit habitats (*pers. observ*.). By directly comparing the presence and absence for contrasting species in the same habitat and artificial light conditions a greater depth of knowledge and evidence can be gained into affects of artificial lighting in the wider environment. In the UK, *Pipistrellus pipistrellus* and *Rhinolophus hipposideros* are sympatric to the south west of England and feed on similar prey; mainly moths and Diptera (Arlettaz et al., 1999; McAney and Fairley, 1989; Racey et al., 1985). *P. Pipistrellus* are common and widespread throughout the UK (Bat Conservation Trust, 2000) and it is assumed that where *R. hipposideros* roosts are present there will be sufficient numbers of *P. Pipistrellus* in the same area to make comparisons between the two species. Through personal experience of undertaking both static monitoring studies and walked transects, where *R. hipposideros* has been recorded, *P. pipistrellus* is invariably recorded. The study investigated the effects of artificial lighting on both species at a broad landscape scale, where bats may have habituated to the lighting regime implemented. Specifically, the study aimed to assess:

1. Whether the number of *P. pipistrellus* and *Rhinolophus* species passes differ in relation to the presence of artificial lighting at a landscape scale.

2. Whether the foraging rate of *P. pipistrellus* (assessd by the feeding buzz to pass ratio and total number of feeding buzzes) differ in relation to the presence of artificial lighting at a landscape scale.

3. Do *P. pipistrellus* and *Rhinolophus species* similarly co-occur, indicating inter-specific competition, in both dark and artificially light conditions**?**

2.3. M*ethods*

2.3.1. Site selection

The study focused on the landscape around *R*. *hipposideros* maternity roosts, to increase the chance of detecting this rare species, whilst *P. pipistrellus* were assumed to be *detected at a* high *rate incident*ally. S**u**rveys were conducted between 8 May and 2 July 2012 at eight *R*. *hipposideros* maternity roosts at a minimum distance of 6.3 km apart, in the south-west of England (Figure 2.1). At each roost bat activity was surveyed within a 2 km radius, excluding the immediate 200 m radius of the roost, since bats may be unable to express avoidance behaviours in this region because of the very limited area available.

As many lesser horseshoe roosts were selected as possible, based on time and equipment restraints. Sites were selected using known roost locations identified by the Vincent Wildlife Trust within the South West region. Using eight sites with 50 detectors at each enabled more power in identifying if there was any significant

effect of artificial light on bat activity and helped to overcome the high variability of bat activity both spatially and temporally. Within each site, detector locations were randomized to avoid patterns in activity due to other factors, such as habitat etc. The implications of using a high number of detectors restricted deployment to using the road network, rather than a grid design.

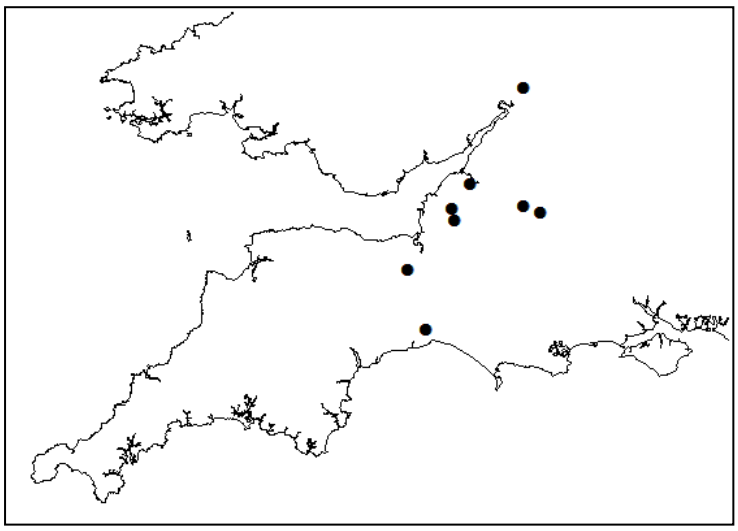

Figure 2.1. Locations of the eight study roosts in the south-west of England.

2.3.2. Acoustic monitoring

At each roost, 50 detectors were randomly positioned at locations of varying light intensities (Figure 2.2), along linear features, using the road network, footpaths and bridleways (each of the eight roosts with 50 detectors, herein referred to as a site). Tree lines and hedgerows were used, since these linear features are known to facilitate movement between resource patches for both genera (Downs, 2006; Schaub, 2007; Verboom and Spoelstra, 1999; Zahn et al., 2008). Detectors were positioned at minimum distance of 100 m apart. Each location was classified by one of three light levels (light, semi-light and dark) based on the distance the detector was from sources of artificial light; light (less than 20 m from streetlight, mean 24

detectors at each site SD 5.6), semi-light (less than 50 m from other artificial light source e.g. housing, security or flood lighting, mean 10 SD 4.1) and dark (more than 50 m from artificial lighting, mean 10 SD 5.2; see section 1.3.4. Light Readings for further details).

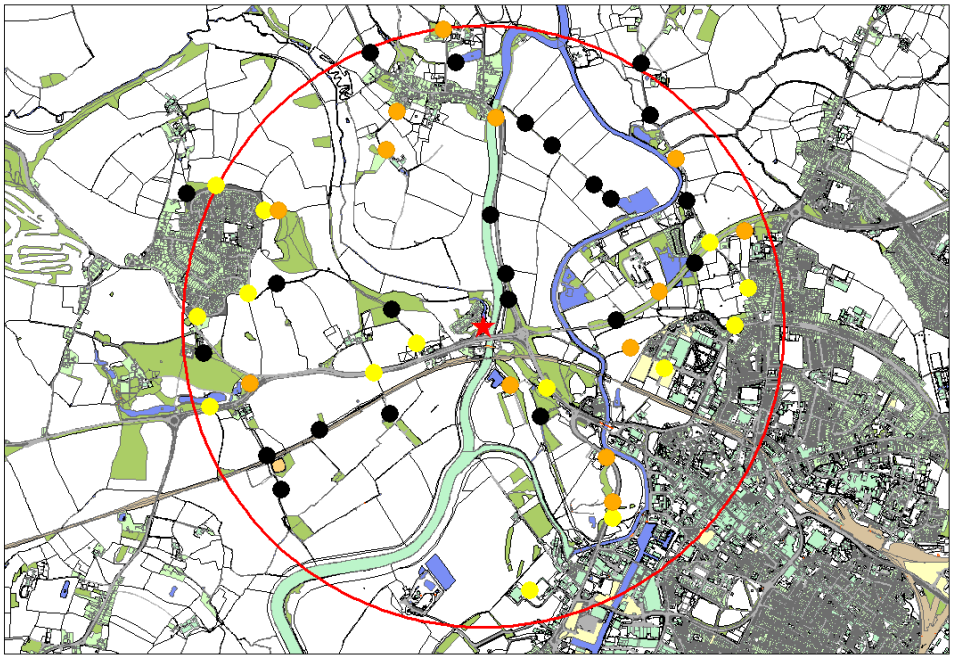

Figure 2.2. An example of the detector positions at one of the study sites. Locations categorised as light (14, yellow), semi-light (13, orange) and dark (23, black) are shown on the map.

Table 2.1 Summary of the number of detectors at dark, semi-light and light locations at each of the 8 roosts in the study.

Roost ID	Dark	Semi-light	Light	Total
1	23	20	3	**46**
2	25	9	11	**45**
3	23	17	8	**48**
4	25	15	7	**47**
5	23	13	13	**49**
6	22	15	9	**46**
7	26	14	7	**47**
8	27	14	6	**47**
Total	**193**	**117**	**61**	**371**

Bat activity was monitored for a mean of 5 nights SD 0.6 at each site, using full-spectrum acoustic detectors coupled with omni-directional SMX-US microphones (Song Meter 2, Wildlife Acoustics, Maynard, USA). Recordings were triggered by a signal to noise ratio exceeding a pre-determined threshold and continued until the threshold was not sustained for a period of at least two seconds. They were programmed to start recording 30 min before sunset and finish 30 min after sunrise.

2.3.3. Bat identification

Kaleidoscope Pro (KPro, v. 1.1.20) was used to automatically classify species, with manual verification conducted for all calls classified as *Pipistrellus pipistrellus* species using parameters taken from Russ (2012). In a previous study (Richardson, 2015) the accuracy of KPro to correctly classify *Pipistrellus pipistrellus* was 93% among a sample of 153,658 calls (S. Richardson 2015, personal communication). A bat pass was defined as a continuous run of pulses for a single individual where pulses were not separated by a gap of more than one second (Fenton et al., 1973). However, for *Rhinolophus* spp., due to their lower detectability yet distinctive call shape, a minimum of one pulse was used to define a bat pass. Uncertain *R. hipposideros* and *R. ferrumequinum* calls were identified to genus (i.e. due to the detectors only recording up to 92kHz, the software inverts the *R. hipposideros* calls and where the frequency modulated portion of the call was absent the two species were not distinguishable).

For *P. pipistrellus,* activity was assessed during the hours of peak activity i.e. the first 2 hours after sunset. The number of *P. pipistrellus* feeding buzzes were also calculated. Additionally, all bat passes across the whole night classified as a *R. hipposideros or R. ferrumequinum* and those classified as an unidentified bat species were manually verified to determine activity levels for *R. hipposideros or R.*

ferrumequinum. Due to the low number of *R. hipposideros* calls and the inability to distinguish some calls apart, analysis was conducted on all *Rhinolophus* spp. and *R. hipposideros* individually.

2.3.4. Light readings

In February 2015 light readings were sampled at each detector locations, where possible, using a broadband light sensor (SpectroSense light meter, Skye instruments, Powys, UK) mounted on the top of a car. The car was driven at approximately 10 miles/hour. Light readings for eight wavelength sensitivities were recorded every two seconds. The average light readings of recordings taken within a 15m radius of each detector were calculated (Figure 2.3). Due to the similarity in lux readings between detectors located in semi-light and dark, these two categories were combined and classified as dark locations for later analyses.

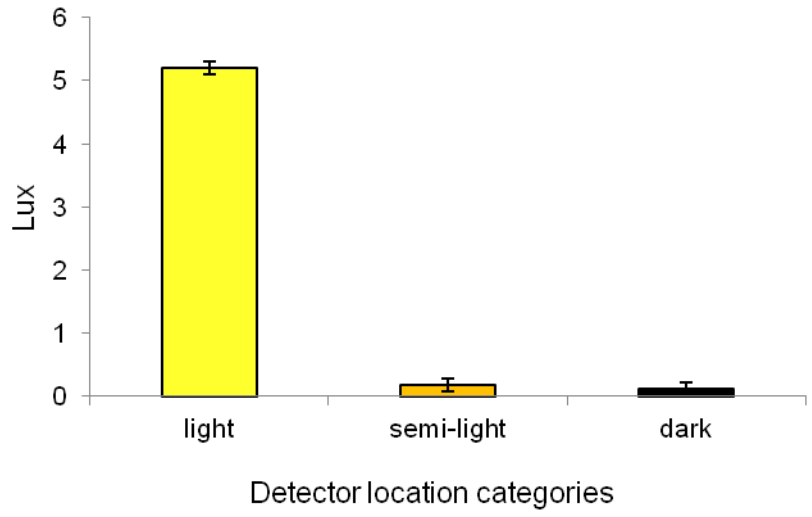

Figure 2.3. Mean (± SE) lux readings for detectors categorised as light, semi- light and dark across all eight study sites.

2.3.5. Habitat analyses

At each detector location, adjacent habitat was categorised according to whether it was pasture or not. Site locations and detectors were digitised in a geographical information system (GIS) using ArcGIS (ESRI ArcMap 10.0). Ordinance Survey vector Mastermap data were used to calculate landscape metrics. The distance from each detector to the nearest woodland (coniferous, deciduous or mixed) and the percentage building cover within a 100 m buffer of the detector (minimum distance between detectors) were calculated. These habitat variables, in addition to pasture, were selected as they are known to be important determinants of foraging activity and density for *Pipistrellus* spp. and *Rhinolophus* spp. (Jenkins et al., 1998, Fuentes-Montemayor et al., 2011; Bontadina and Schofield, 2002; Walsh and Harris, 1996).

2.4. Statistical Analysis

All statistical analyses were conducted using R (v.3.1.1), with the glmmADMB package (v. 0.8.0). Graphs were produced using ggplot2 (v.1.0.0). Collinearity was assessed between all predictor variables; if $R < 0.6$ and p-value > 0.05 both predictors were included in models. Where predictors were correlated, separate models were run for each predictor and the predictor with the highest coefficient was selected for the final model. Although light level co-varied with some habitat variables (percentage building cover and pasture) , both were retained in the model, since if the factor light level was highly significant an effect would be found. The residuals of all models were assessed to ensure there was no evidence of heteroscedasticity and that standardised residuals were normally distributed.

A generalized liner-mixed effects model (GLMM) with a negative binomial error structure was used to model the total number of *P. pipistrellus* passes in the

first two hours after sunset per night,fitted as the dependent variable. The following predictor variables were assessed: light level (factor two levels: light and dark), pasture (factor two levels: presence, absence), building cover (% within a 100 m radius of the detector) and minimum distance to woodland (m). Since activity at each habitat predictor may vary dependent on the light category, two-way interactions between light category and each habitat variable were assessed. Site, detector nested within site and night were fitted as random effects to account for the temporal and spatial autocorrelation in the dataset (Zuur et al. 2009). Due to the low number of *Rhinolophus hipposideros* passes recorded, all *Rhinolophus* species passes were combined for subsequent analyses. The same model structure and fixed and random effects was used to model the total number of all *Rhinolophus* spp*.* passes per night, fitted as the dependent variable.

To assess if *Rhinolophus* spp. and *P. pipistrellus* co-vary, possibly indicating that there is inter-specific competition*,* a GLMM with a negative binomial error structure and logit link function was used to determine if *P. pipistrellus* activity was a significant predictor of *Rhinolophus* spp. activity. *Rhinolophus* spp. activity was restricted to the first two hours after sunset to correspond with *P. pipistrellus* activity and fitted as the dependent variable. Site, detector nested within site and night were fitted as random effects. This was assessed for all detectors combined and in a separate model for only those detectors located in dark locations due to the very low *Rhinolophus* spp. activity at street lit locations. All confidence intervals for model predictions are given as 95%.

2.5. Results

2.5.1. All species summary

Bat activity was assessed for 351 detector nights in light locations and 1,262 in dark locations (totalling 1,613 detector nights; Table 2.1). During the first two hours after sunset the number of passes recorded for *P. pipistrellus* was 81,246 and 1,507 for *Rhinolophus* spp. during the entire night. Among *Rhinolophus* spp. passes, 623 (53%) were *R. hipposideros*, 801 (41%) *R. ferrumequinum* and 83 (6%) *Rhinolophus* spp. (unidentified to species).

Table 2.1. The mean number of passes ± SE per detector night across sites recorded for each species at light and dark locations across 8 sites. For *P. pipistrellus* passes are given for the first two hours after sunset.

	Nights	Dark (±SE)	Light (±SE)
P. pipistrellus	2 hours	44 (8)	41 (12)
Rhinolophus spp.	Full	1.2 (0.5)	0.2 (0.1)
R. hipposideros	Full	0.5 (0.2)	0.04 (0.01)
Rhinolophus spp.	2 hours	0.8 (0.3)	0.1 (0.04)

2.5.2. P. pipistrellus

There were no significant predictors, including the light category, for the number of *P. pipistrellus* passes per night across the eight sites. The feeding buzz ratio was 35% higher in dark locations (0.03 passes per detector night ± SE 1.17) compared to at street lit locations (0.02 ± SE 1.29), which differed significantly ($\chi^2 = 4.90$, $P = 0.027$, Figure 2.4). As the percentage cover of housing increased the feeding buzz ratio also increased at both dark and street light locations (Figure 2.5, $\chi^2 = 10.62$, $P = 0.001$). The presence of pasture adjacent to the detectors did not have a significant effect on the feeding buzz ratio.

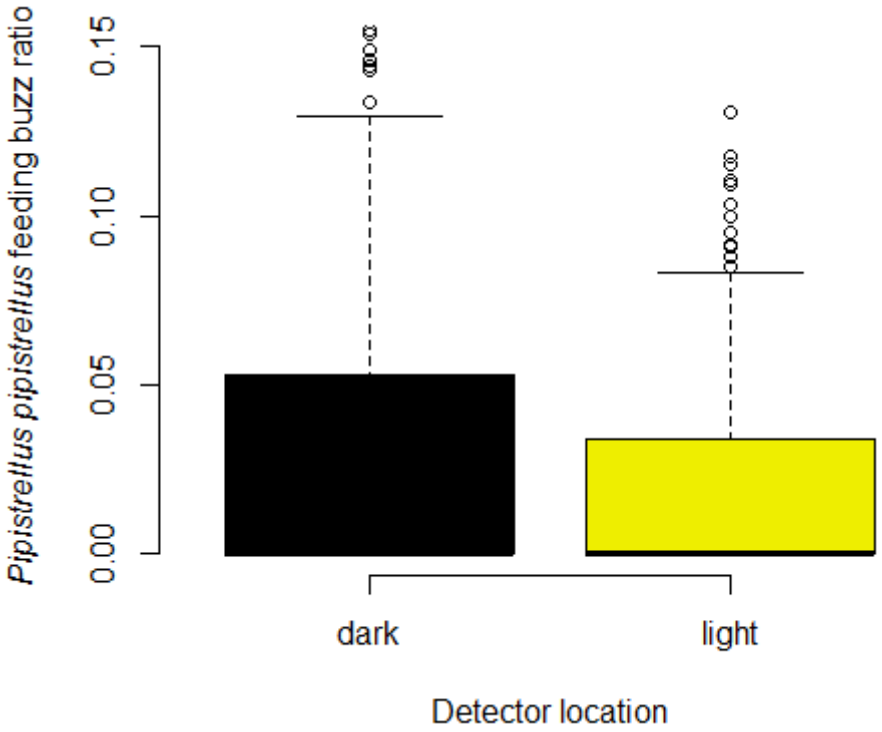

Figure 2.4. *Pipistrellus pipistrellus* feeding buzz ratio per detector night in relation to the location of detectors at dark and street lit locations across 8 sites.

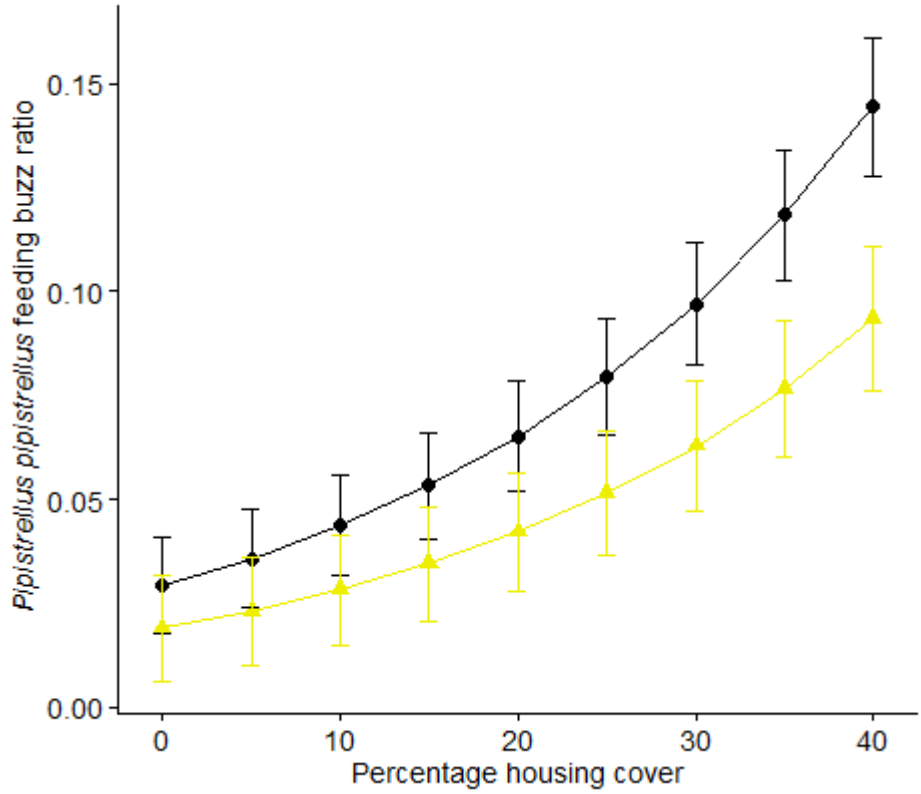

Figure 2.5. Predictions from a GLMM of *Pipistrellus pipistrellus* feeding buzz ratio per detector night in relation to the percentage housing cover for dark (blue line) and street lit (yellow line) locations across 8 sites.

2.5.3. Rhinolophus spp.

Rhinolophus spp. passes were only significantly predicted by the presence of a street light (χ^2 = 27.18, *P* = <0.001). The mean number of passes was 79% higher at dark locations (0.21 ± SE 1.00 passes per detector night), than at street lit locations (0.04 ± SE 1.00, Figure 2.6). Distance to woodland (χ^2 = 3.72, *P* = 0.054) and pasture (χ^2 = 3.76, *P* = 0.052) were close to having a significant effect on *Rhinolophus* spp. activity. *Rhinolophus* spp. passes increased with reduced distance to woodland for both street lit and dark locations and passes were increased at detectors (all locations) adjacent to pasture.

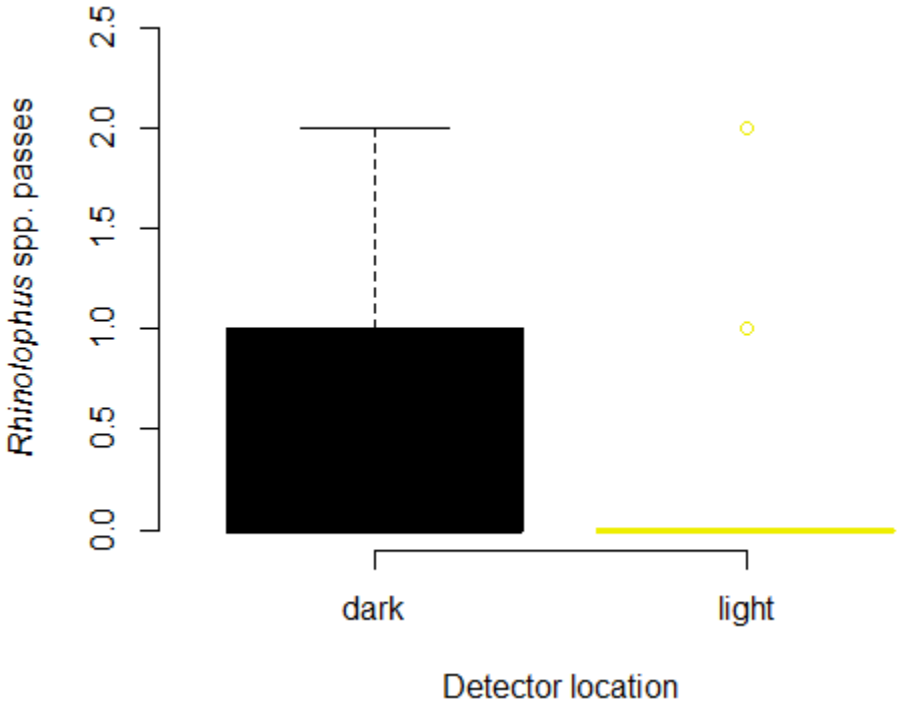

Figure 2.6. *Rhinolophus* spp. passes per detector night in relation to the location of detectors at dark and street lit locations across 8 sites.

2.5.4. Inter-specific species interactions

The number of *P. pipistrellus* passes was a significant positive predictor of the number of *Rhinolophus* spp. passes ($P < 0.001$[1]). This relationship was similar when only considering the detectors located in dark locations ($P < 0.001$).

2.6. Discussion

Little is known about how mammals, particularly nocturnal ones, are able to adapt to increasing exposure to artificial light (Beier, 2006). It is essential to understand how different species respond, so that mitigation measures can be properly addressed. Activity levels were monitored in relation to light level in the wider landscape for two

[1] χ^2 values are not obtainable since alternative models with the fixed factor 'light' excluded did not converge and hence anova tests were not possible. P-values are extracted directly from the summary of model outputs of the full model.

genera of bat widely thought to have different tolerances to artificial light. For *Rhinolophus* spp., most activity occurred in dark locations, away from street lights, whereas *P. pipistrellus* activity did not vary in relation between dark and street lit locations, but there foraging rate was lower in street lit locations. These results show that artificial lighting at a landscape scale may adversely affect both species, either directly through reducing the available foraging habitat and access to it, or indirectly by reducing the rate of foraging, possibly linked to insect composition being altered at street lit locations.

Differences between the genera were also found with respect to habitat preferences and building cover. *P. pipistrellus*, had similar activity regardless of the presence or absence of adjacent pasture, the distance to woodland, or the density of housing. However, the presence of pasture and close proximity of woodland was an important determinant of *Rhinolophus* spp. activity. These results support that Pipistrelle spp. are considered generalists and are found in a wide array of habitats. whereas, Rhinolophus spp. are considered specialists requiring particular habitat features. Presence and activity levels in the landscape are determined by a difference in light tolerance between the two genera, related to predation risk, as well as habitat requirements for foraging based on their respective differences in call structure.

In terms of *P. pipistrellus* foraging, there was a positive association with building cover. This association could be attributed to increased roosting and foraging opportunities. The human built environment provides roosting opportunities for some species of bat (Kunz, 1982; Dietz et al., 2009) and *P. pipistrelle* are one of several species in Europe that have adapted to the built environment (Duchamp et al., 2004; Ancillotto et al., 2015) as natural roosts have become scarcer. This

adaptation to urban environments has been recently highlighted in Italian populations of *Pipistrellus kuhlii* where an increase in skull size has been recorded since world War II (Tomassini et al., 2014). This rapid evolution is thought to be an adaptation to the rapid increase in artificial light linked to urban expansion, facilitating a change to larger prey items (*Lepidoptera* rather than *Diptera*) attracted to street lights. Other studies on *P. kuhlii* have also found a preference for street light foraging (Barak and Yom-Tov, 1989; Schnitzleret al., 1987). In addition, this species has been found to be more successful at producing young in urban areas with artificial street lighting, were concentrations of insects can be exploited (Ancillotto et al., 2015).

The results presented here suggest that no such foraging preferences are found for *P. pipistrellus*. Although many observations and studies have identified *Pipistrellus* spp. foraging around street lighting, a preference for foraging in non-artificially lit locations was found across the eight sites in this study. However, *P. Pipistrellus* activity did not significantly differ between artificially light and dark locations, indicating that this species is indeed light tolerant but prefers, or has more opportunity to forage in dark locations for appropriate prey items. Perhaps *P. pipistrellus* is too small to take advantage of the increased numbers of *Lepidoptera* attracted to street lights, compared to *P. kuhlli* which has evolved to hunt these larger prey items. Further work to sample invertebrate abundance and species composition at streetlights compared to dark locations is required to verify if *P. pipistrellus* are choosing dark locations to forage in preference to artificial lights. Other studies have also found a preference for non street lit environments for this species. *P. pipistrellus* were rarely encountered near street lamps in Sweden (Rydell, 1992), although this was attributed to possible competitive exclusion by the larger *Eptesicus nilssonii* present in the study area. More recently, (Hale et al., 2015)

recorded *P. pipistrellus* flying in an urban environment, between vegetation gaps and found a preference for darker gaps and lower lighting thresholds for larger gaps.

The positive association of percentage building cover and *P. pipistrellus* foraging found in the present study is perhaps explained by both a strong association for roosting opportunities within buildings and the rural and semi urban environment found across the study sites, where insect generation is expected to be high. Building cover in low densities may provide some shelter for insects in much the same way as trees and natural linear features such as hedges. Buildings are a preferred roosting location for *P. pipistrellus* (Thompson 1992) and in combination with increased foraging opportunities for *P. pipistrellus* around buildings in a rural environment, a positive correlation in the model was found. In fact, the study site with the highest percentage of manmade surfaces was 10%, of which buildings constituted 4%, and so predictions of the effect of buildings from the model are unreliable beyond these percentages.

Periods of foraging activity for an insectivorous bat have been calculated to account for only 15-17 % of the daily time budget but are the largest component of the average daily energy budget, at above 60 % (Kurta et al., 1989). Bats have a very high energy requirement compared to terrestrial mammals (Thomas, 1975) and take advantage of concentrated resource patches (Aldridge and Rautenbach, 1987; Bell, 1980; Ries et al., 2004) important for survival. Artificial lighting is known to attract insects in large numbers (Blake et al., 1994; Rydell and Racey, 1995; Rydell, 1991) and as such provides a reliable opportunity for bats to relinquish the high energy demands of foraging. However, this study shows that the foraging rate is increased in dark locations compared to street lit locations. This suggests that the quantities of suitable insect prey items are not sufficiently increased at street lights

compared to dark locations to attract more *P. pipistrellus* to a focal point of foraging than in dark areas.

From personal observations, as well as other studies referenced above, it is clear that *P. pipistrellus* do feed around street lamps but feeding in the dark is perhaps more profitable and less risky in terms of predation, just not as observable to humans. In many studies bat activity is used as an estimate of the number of individuals due to the inherent difficulty of recording numbers of a highly mobile nocturnal species. It is possible that an single bat making multiple passes may register in one unit of time the same number of passes on a detector as an equivalent number of individuals making one pass. Some further investigation into standardizing activity levels may more accurately determine pass rates as described by Miller (2001).

For *Rhinolophus* spp., percentage building cover was not significant at predicting activity, however, *P. pipistrellus,* which feeds on similar prey to R. hipposideros (Arlettaz et al., 1999; McAney and Fairley, 1989; Racey et al., 1985), were shown to be feeding at an increased rate as building cover increased. Threlfall *et al.* (2011), found that insect biomass and bat foraging were lowest in high density housing areas which was attributed to an increase in large impermeable surface area, leading to low primary productivity of insects. This is understandable in highly urbanized locations but is not the case in the rural and semi urban sites in this study. At a local (100 m radius of detector locations) and landscape scale (2 km radius of roost), on average, 10.7% (±SE 0.7%) and 4.9% (±SE 1.0%) of the total area of sites were classified as 'manmade' respectively, hence, non-artificial surfaces, suitable for supporting insect populations was not considered to be in short supply across the study areas.

The higher numbers of *Rhinolophus* spp. bats recorded away from building cover can be explained by their foraging ecology and preference for woodland clutter environments (Bontadin et al., 2002). With increasing distance to woodland, the number of *Rhinolophus* spp. passes decreased. *Rhinolophus* spp. are commonly associated with woodland environments and are rarely found in urban areas. In part, this is likely due to their wing morphology and echolocation call design which constrains open site foraging, but aversion to light is also likely to be a major factor. This study found that passes for *Rhinolophus* spp. will be highest when close to woodland, when pasture is close by, and away from street lit locations. This may be attributed to the increased number of invertebrates generated by pasture habitat (c.f. arable and non-natural surfaces) and the benefits of woodland and hedge networks associated with pasture fields facilitating commuting routes.

This study further supports evidence that *Rhinolophus* spp. avoid artificially light environments (Ramovš et al., 2010; Stone et al., 2009; 2012). In the present study, *Rhinolophus* spp. activity was investigated within realistic levels of lighting, at a wide spatial scale and the results show an avoidance of artificial lighting across the wider landscape. Even for the more anthropogenically-robust *P. pipistrellus*, artificial lighting was associated with reduced foraging activity. While *P. pipistrellus* have adapted to an increasing human built environment by utilizing roosting opportunities, the increasing artificial lit environment may be a more difficult adaptation.

The Habitats Directive (1992/43/EEC) legally protects bat roosts within the European Union, however, the level of protection given to commuting routes is less clear (Garland and Markham, 2007). Maintaining or increasing important habitats in eroding dark landscapes is a key priority, yet light pollution is seldom considered in habitat management plans. The negative effects of artificial light shown here and in

other studies should be considered when infrastructure and housing developments plan to increase the amount of artificial light in the environment.

Chapter 3:

3. An experimental approach to assess the effects of artificial lighting on bat activity

3.1. Summary

There is increasing knowledge that artificial light adversely affects many species, particularly nocturnal animals, such as bats. Understanding the behavioural responses of bats to different types of artificial lights in the landscape may aid in the optimal development of lighting technologies. With the trend toward artificial lighting becoming more broad spectrum, it is likely that this will have a negative effect on a greater number of species. A series of fixed lighting experiments were conducted, to compare bat activity during three treatments, dark, UV-LED lighting, and filtered UV-LED lighting. Bat activity was monitored at the treatment locations and at adjacent dark hedgerows, for a duration of 12 nights, at each of five sites in South West England. There was only sufficient activity to consider the two most common species in the UK, *P. pipistrellus* and *P. pygmaeus.* No significant affects of treatment type were found, nor was bat activity significantly altered at adjacent dark hedgerows. This may be due to the high variability of bat activity, insufficient replicates or insufficient differences between the light types, to find any significant effects. It may also show, similar to the previous chapter, that *Pipistrellus* spp. are relatively tolerant of artificial lighting in terms of recorded activity. Extending the research to encompass a greater time frame and number of sites may help to understand responses for a wider range of bat species to different artificial light spectra.

3.2. Introduction

Natural habitats are becoming increasingly threatened due to an expanding human population (Cincotta et al., 2000). Urbanisation is one of the key drivers associated with species endangerment (Czech et al., 2000). By 2030, 60% of urbanization is expected to occur within 50 km of protected areas and biodiversity hotspots (Güneralp and Seto, 2013) and by 2050 two-thirds of global populations will be living

within urban areas (United Nations, 2014). With increasing urbanization comes an increase in artificial light, estimated at an annual rate of 6% (Hölker et al., 2010). Light pollution, to date has received little attention. For example, less than two percent of scientific papers on pollution published between 2010 and 2015 researched light pollution[2].

Despite the relatively limited amount of research on the effects of light pollution, artificial light has been shown to influence the foraging behaviour (Kuijper et al., 2008; Stone et al. 2009; 2012), reproduction (Rand et al., 1997), growth, sexual maturation (Oppedal et al., 1997) and communication (Longcore and Rich, 2004), of a range of taxa. With an increasingly illuminated world, light sensitive species in or near highly illuminated urban areas at risk of local extinction (Hölker et al., 2010). Among species affected by artificial lighting, nocturnal animals are considered to be particularly vulnerable. Nearly all bats are nocturnal (Speakman, 1991) and considered important bioindicators (Jones et al., 2009) and as such are a good model taxon for investigation of the effects of artificial lighting.

The movement of many bat species between resource patches is often facilitated by linear features, such as tree lines and hedges, which are frequently used as foraging sites where congregations of insects are formed (Racey et al., 1985; Brigham et al., 1997; Verboom and Huitema, 1997, Grindal and Brigham, 1998, Verboom and Spoelstra, 1999). Disturbance of these commuting and feeding areas may therefore have significant consequences on flight and foraging behaviour, and ultimately population survival (Kuijper et al., 2008). Disruption of commuting routes, in terms of artificial lighting, is particularly important for bat species considered to be negatively phototaxic, whereby highly illuminated sections of a

[2] Web of Science; search terms in title: air OR water OR noise OR light AND pollution; document type: article and review in English.

linear feature, such as a hedgerow, may be effectively fragmented. Previous studies have shown that artificial light can cause significant local reductions in bat activity for some species (Kuijper et al., 2008, Stone et al., 2009; 2012). Artificial lighting could also cause a trophic mismatch between positively phototaxic insects and negatively phototaxic bats (Arlettaz et al., 1999).

Resident bat species in the UK are all insectivorous and can be broadly categorised into light-shy or light-tolerant based on physiological characteristics such as wing morphology and echolocation call structure (Neuweiler, 1989). Narrow winged, fast, open space fliers have lower echolocation frequencies and are more tolerant of light, whereas broad winged, slower, clutter fliers have higher call frequencies and are less tolerant of light (Neuweiler, 1989; Jones and Rydell 1994). Differing physiological characteristics therefore allow certain species to exploit congregations of insects around street lamps (Haffner and Stutz 1985; Barack and Yom-Tov 1989; Rydell, 1992; Blake et al., 1994, Russo and Jones, 1999), whereas artificial lighting can cause disruptions to roosting behaviour (Downs et al., 2003, Ramovš et al., 2010), delayed roost emergence (Downs et al., 2003) and compromised commuting and reduced activity for light sensitive species (Stone et al. 2009; 2012; McGuire and Fenton, 2010). In the UK, *Pipistrellus pipistrellus* and *Eptesicus serotinus* have both been recorded foraging near or at street lamps (Blake et al., 1994). In contrast *Rhinolophus*, *Myotis* and *Plecotus* spp. have been shown to be negatively affected by artificial light (Furlonger et al., 1987; Rydell, 1992; Stone et al. 2009; 2012). In addition to the direct avoidance of artificial light by light-shy species, there is likely to be an indirect relationship between bat foraging behaviour and light-induced changes of their insect prey. Artificial lights attract airborne insects; however, the degree of attraction varies depending on insect species, type of light,

distance from light source and changing background illumination (Eisenbeis, 2006; Rydell, 1992; van Langevelde et al. 2011; Somers -Yeates 2013). Such changes in insect activity may significantly influence feeding opportunities for both light shy and light tolerant bat species, within the immediate vicinity of the light source, as well as the wider surrounding environment.

Two of the largest sources of artificial light are street lighting and illuminated sports fields (Luginbuhl et al., 2009). Different types of widely used light vary in wavelength composition. Shorter wavelengths and higher UV content is particularly disruptive to insects (Rydell, 1992; Eisenbeis, 2006; van Langevelde et al., 2011). Stone et al. (2009, 2012) used high-pressure sodium (HPS) and LED lamps respectively to study the effect of artificial lighting on *R. hipposideros* commuting routes within 1km from maternity sites. A significant reduction in *R. hipposideros* activity was found at artificially lit areas, with similar patterns also found for *Myotis* spp. *Pipistrellus* spp. and *Eptesicus/Nyctalus* spp. activity rates were unaltered by lighting. In previous studies bat activity has only been assessed directly at the artificial light source (whether observational or experimental studies) and not at distances further away to determine whether alternative commuting and foraging strategies are adopted when artificial lighting is erected in the landscape.

To improve knowledge of how bats use commuting and foraging features in proximity to artificial lighting, a series of fixed lighting experiments were conducted, whereby lighting conditions were manipulated and the effects on both foraging and flight behaviour investigated. To replicate the spectral qualities of conventional street lamps but without introducing the noise produced by the generators employed in previous research, 12V battery-powered lamps were used. To simulate metal-halide lighting, which is widely used in street-lighting, a UV chip was installed into a LED

lamp. The resulting lamp could then be modified with an addition of a UV filter covering to provide two lamp types of varying UV intensity. Specifically, this study aimed to answer the following questions:

1. Does activity and foraging rate vary between dark, UV-LED artificial lighting and UV-filtered LED artificial lighting and does this differ between species?
2. Does activity and foraging rate vary between the artificially illuminated position (both UV-LED and UV-filtered LED) and adjacently positioned unlit hedges of similar habitat?

3.3. Methods

3.3.1. Study sites

Lighting experiments were conducted at five sites in Devon, England (Figure 3.1) where good commuting and foraging habitats were present. All sites were characterized by having ancient hedgerows connected to deciduous woodland in naturally dark environments with low levels of urbanization within 2km of the site.

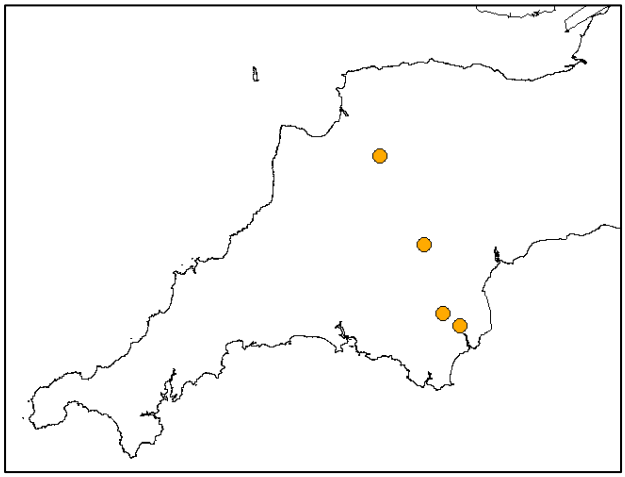

Figure 3.1. Location of sites (n = 5, the northern point includes two sites located 1km apart) in Devon, England.

3.3.2. *Replicating metal halide lights*

Metal halide lights are commonly used as a method of street lighting (Gaston et al., 2013, Davies et al., 2013), but require high voltages to operate. Since a 12v battery system (Yusa Battery Sales Limited, Swindon) was used in this study to power the lights, light options were limited to LED and Halogen (which do not contain elements of the UV spectrum). Therefore, an 18W lamp (THG Ltd.) containing six Cree LED chips was used with one of the Cree chips replaced with a UV specific chip (WEPUV3-S2 UV Power LED, Winger, Germany) to obtain a lamp with a spectral composition containing an element of UV wavelength. The UV intensity of the lamp could then be varied by attaching a UV film filter (226 Lee Filter, leefilters.com, Andover, Hants, UK) to the lamp lens, reducing UV intensity by approximately 40% and altering the spectral composition (Figure 3.2). This modified lamp produced an intensity reading of 64.5 lx at a distance of 5m using a lutron LX-1108 light meter (the standard lamp produced 68.4 lx at 5 meters).

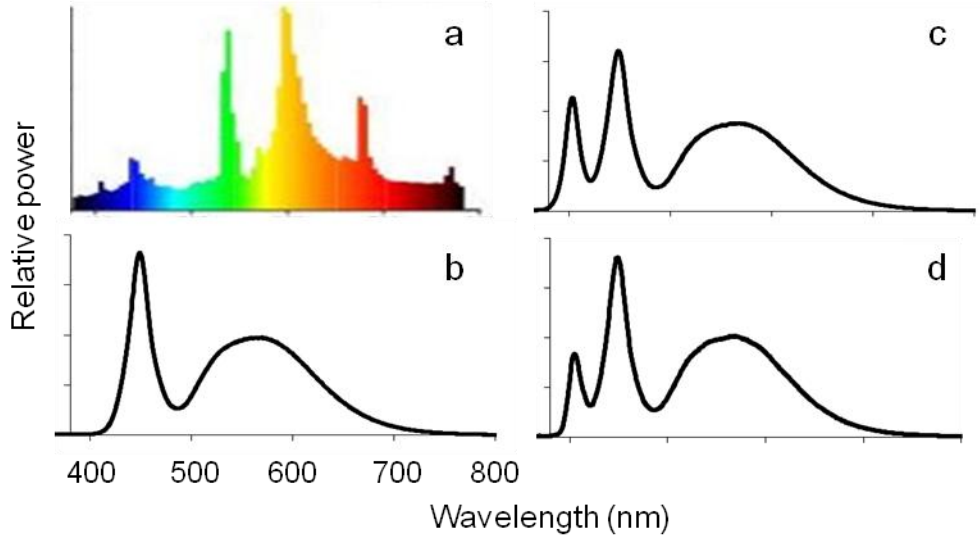

Figure 3.2. Wavelength compositions of a typical metal halide street light (a) and standard 18 Watt Cree LED lamp (b). Treatment lights used in the study are (c) Cree LED-UV lamp and (d) Cree LED UV-filtered lamp. Relative powers are comparable

for b-d, whereas typical metal halide street lights (a) are 45-60 Watt and hence not directly comparable to Cree LED.

3.3.3. Study design

The study was conducted between 29 July and 21 October 2014. At each site two modified lamps were erected to simulate a pair of street lights. The lamps were mounted on two tripods or fastened to the limbs of trees at heights of approximately 5m and positioned 15m apart along one side of a linear feature. Bat activity was monitored at heights of ~1.5m at three positions for each experiment; the artificial light treatment position (study aim 1 and 2) and at two adjacent linear features which were not artificially lit (herein referred to as dark non-treatment positions (study aim 3) (Figure 3.3). The light treatments were randomised over a twelve-day period, depending on weather conditions, with a minimum of 3 nights of each treatment: no lighting (control), full UV-lighting and UV-filtered lighting, at each experiment site. During the control treatment, all equipment was kept in place (lamps and tripods). Lighting treatments started at sunset and continued for a period of 3 hours, coinciding with peak bat activity (Swift, 1980; Rydell et al., 1996).

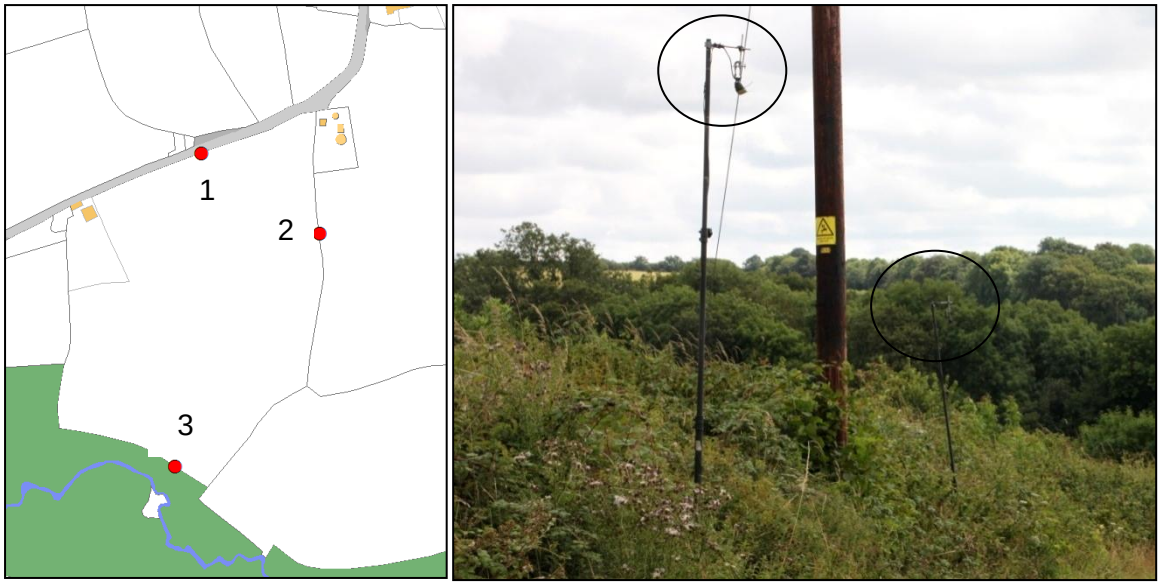

Figure 3.3. Layout of the experimental design at one of the five sites. Position 2 is the location of the light treatment (dark, UV-LED and UV-filtered LED) and position 1 and 3 are the locations of the two dark controls. In the photograph the lights in position 2 are shown (circled in black) with the bat detector located between them.

Table 3.1. Example of rotation of treatment rotations for the three positions for experiment 1. For each treatment 3 nights minimum were conducted. Treatments; 0 =Dark , 1 = UV filtered , 2 = UV.

Experiment	Position	Treatment	Light
1	1	2	0
1	2	2	1
1	3	2	0
1	1	0	0
1	2	0	1
1	3	0	0
1	1	1	0
1	2	1	1
1	3	1	0

Song Meter 2 (SM2, Wildlife Acoustics, MA, USA) bat detectors with omni-directional SMX-US microphones were used to record activity. The detectors were programmed to be triggered when the signal to noise ratio was above a pre-determined threshold (here: 18db to 48db) and until the threshold was not sustained for a period of at least two seconds.

3.3.4. Bat identification

Files were processed using Kaleidoscope Pro (KPro) software (v. 1.1.20) with British classifiers (v.1.0.5). Noise was filtered out and all potential bat files were manually verified. Bats were identified to species with the exception of *Myotis* spp. and *Plecotus* spp. which were identified to genus (due to the similarity of their call structures) using call parameters given in Russ (2012). A bat pass, equivalent to an individual file, was defined as a continuous run of pulses not separated by a time gap of more than one second (Fenton et al., 1973). All passes within a file were counted, including feeding buzzes.

3.3.5. Environmental indicators

Weather variables, including rainfall (mm), temperature (°C), relative humidity (%) and wind speed (m/s) were monitored and recorded automatically using a wireless weather station. Acoustic recording and analysis were only considered for nights of good weather (no rainfall, wind speed < 8 m/s and temperatures above 10 °C during treatment period).

3.4. Statistical analysis

Analysis was only possible on data generated at three of the sites (1,4 and 5) due to partial equipment failure at two of the sites (2 and 3). Statistical analysis was conducted using R (v.3.1.1). When parametric models were used (negative binomial linear mixed models) there was high over dispersion (theta >10) despite using an observational level random effect and a negative binomial error distribution (Appendix: Figure 1). This was due to the high variance relative to the mean, as a result of a low sample size. Non-parametric tests were therefore chosen. A Friedman test (non-parametric alternative to the one-way ANOVA) was conducted to assess whether there were any significant differences between the number of *P. pipistrellus* passes, the number of feeding buzzes and the ratio of feeding buzzes to passes for each lighting scenario (control, UV-filtered lighting, and full UV-lighting) at only the treatment position across the three sites (included as a blocking factor). The Friedman test was repeated for *P. pygmaeus*. Analysis on other species was not conducted due to a low pass rate. Further Friedman tests were conducted to assess whether activity differed at the two dark non-treatment positions (combined) compared to the single artificial light treatment position. This test was repeated for each treatment scenario (dark, UV-filtered lighting, and full UV-lighting) for; the

number of *P. pipistrellus* and *P. pygmaeus* passes, the number of feeding buzzes and the feeding buzz ratios.

3.5. Results

Bat activity was monitored over a total of 82 nights (27 dark, 25 UV-filtered lighting and 30 full UV-light), recording 6,176 bat passes (excluding two sites with equipment failure). Twelve species were recorded across sites with *P. pipistrellus* and *P. pygmaeus* being the most common; accounting for 93% of all passes (62% and 31% respectively, Table 3.2). Overall, *P. pygmaeus* feeding rates were higher than for *P. pipistrellus*, both in terms of the absolute number of feeding buzzes and the ratio of feeding buzzes to passes (Table 3.3).

For *P. pipistrellus* and *P. pygmaeus* there was no significant effect of the lighting scenario treatment (dark, UV-LED or UV-filtered LED) on the number of passes ($\chi^2 = 0.67$, $P = 0.717$, $\chi^2 = 4.67$, $P = 0.097$, respectively). There was no significant difference between activity at the dark non-treatment positions (two unlit adjacent hedgerows) and the light treatment position for all three light scenarios (dark, UV-filtered light and light) for both *P. pipistrellus* and *P. pygmaeus* ($\chi^2 = 0.33$, $P = 0.564$ for all test results). The number of feeding buzzes and the feeding buzz ratio were correlated with the number of passes (*P. pipistrellus*: R = 0.81, $P < 0.001$, R = 0.49, $P < 0.001$, respectively; *P. pygmaeus*: R = 0.82, $P < 0.001$, R = 0.56, $P < 0.001$, respectively) and hence statistical tests were not conducted.

Table 3.2. Summary of the mean number of passes (± SE) per night (3 hours) for all species detected at the single light treatment position and at the two dark non-treatment positions. Three treatments (dark control, full UV-light, UV-filtered light) were tested across three study sites in Devon, England. The species considered for analysis are highlighted in bold.

	Treatment location			Non-treatment locations			
Species	Control	Filtered UV-light	Full UV-light	Control	Filtered UV-light	Full UV-light	Total passes (%)
B. barbastellus	0.3 (0.2)	0.3 (0.3)	0.8 (0.6)	0.5 (0.4)	0.7 (0.3)	1.0 (0.6)	33 (1)
E. serotinus	0.1 (0.1)	0.4 (0.3)	0.8 (0.6)	0.1 (0.1)	0.5 (0.3)	1.0 (0.6)	15 (<1)
Myotis spp.	0.9 (0.5)	1.4 (0.4)	1.2 (0.4)	1.7 (1.4)	2.1 (0.9)	2.5 (0.7)	170 (3)
N. noctula	1.3 (0.9)	2.3 (0.7)	1.8 (0.7)	2.3 (1.4)	2.8 (1.3)	1.6 (0.5)	170 (30)
P. nathusii	0 (0)	0.3 (0.3)	0.7 (0.7)	0 (0)	0.5 (0.3)	0.8 (0.6)	6 (<1)
P. pipistrellus	**122 (88)**	**64 (44)**	**155 (109)**	**12 (1)**	**24 (8)**	**12 (3)**	3,840 (62)
P. pygmaeus	**5 (3)**	**85 (78)**	**34 (29)**	**10 (5)**	**18 (12)**	**12 (5)**	1,920 (31)
Plecotus spp.	0 (0)	0.3 (0.3)	0.9 (0.6)	0 (0)	0.3 (0.3)	0.7 (0.6)	4 (<1)
R. ferrumequinum	0.3 (0.3)	0.7 (0.3)	0.7 (0.7)	0 (0)	1.0 (0.6)	0.7 (0.7)	4 (<1)
R. hipposideros	0 (0)	0.3 (0.3)	0.7 (0.7)	0.2 (0.2)	0.3 (0.3)	0.8 (0.6)	6 (<1)
						Total passes	**6,168**

Table 3.3. Summary of the mean (± SE) feeding buzzes per night (3 hours) for *P. pipistrellus* and *P. pygmaeus* at the single light treatment position with three treatments (dark control, full UV-light, UV-filtered light) and at the two dark non-treatment positions, across three study sites in Devon, England.

		Treatment			Non-treatment			Total FB (%)
Species		Control	Filtered UV-light	Full UV-light	Control	Filtered UV-light	Full UV-light	
P. pipistrellus	Absolute	7 (4)	10 (9)	4 (3)	1 (0)	3 (0)	2 (1)	294 (48)
	Ratio	0.04 (0.02)	0.22 (0.15)	0.04 (0.02)	0.05 (0.01)	0.10 (0.01)	0.12 (0.02)	
P. pygmaeus	Absolute	0 (0)	8 (7)	2 (1)	3 (2)	5 93)	3 (1)	318 (52)
	Ratio	0.03 (0.03)	0.09 (0.05)	0.16 (0.09)	0.17 (0.04)	0.12 (0.06)	0.12 (0.06)	

3.6. Discussion

The use of new energy efficient street lighting technologies has been implemented with little research on the effects to nocturnal wildlife. The latest technologies such as metal halide and LED are both, energy efficient and low maintenance, offering a broad spectrum which provides improved colour rendering for human vision compared to traditional LPS and HPS. In this study, UV modified LED lamps (replicating metal halide lighting) were used to assess the impact of modern artificial lighting on bats. There was no effect of full UV-LED or UV-filtered LED lighting on the number of passes or foraging rate for both *P. pipistrellus* and *P. pygmaeus.* This supports Stone et al. (2012) where standard white LED technologies were tested and no effects on Pipistrelle spp. activity or feeding were found. This is perhaps somewhat surprising given that the LED lights used in this experiment where adapted to include a UV component of the spectrum, known to attract insects, unlike Stone et al. (2012) which used LED lights without a UV component. Bats are known to be loyal to foraging routes, and hence erecting lights over a short period of time may not always alter their behaviour, particularly generalist species, such as Pipistrelle spp., especially given that there are many factors governing bat distribution and abundance, such as, natural congregations of insects, microclimate, habitat, predator avoidance and roost availability (Fukui et al., 2006; Threlfall et al., 2012).

The results in this study are in contrast to several studies of older white lighting technologies, such as High Pressure Mercury Vapour (HPMV), which emit UV light, where Pipistrelle spp. and other light tolerant species were found to be more active in terms of passes and feeding at street lights compared to dark sites (Rydell, 1992; Blake et al., 1994; Rydell and Racey, 1995). With a bigger study

design (more sites, nights and perhaps more intense lighting), this experiment may have provided more substantial evidence for avoidance or attraction to certain types of lighting. The data collected was not sufficient to overcome the high variability in bat activity and no strong effect of the artificial lighting was determined.

3.6.1. Limitations and future research

The experiment took place over a 12-week period, however, sites could only be sampled consecutively rather than simultaneously due to equipment resources. Across the whole experiment period, a full cycle of the lunar phases occurred three times but each site was sampled at a different period of the lunar cycle. Changes in ambient light levels, such as moonlight, have been shown to influence both bat and insect activity as well as alter the influence of artificial light sources (Fenton et al., 1977, Rich and Longcore, 2006). A study of bat activity in the Sengwa Wild Life Research Area, Zimbabwe by Fenton et al. (1977) found that three species of insectivorous bat in the study area altered their foraging patterns on bright moonlit nights. This was thought to be in response to the higher predation risk by the endemic bat hawk (*Macheiramphus alcinu*). Lunar-induced changes in insect distribution and abundance have also been shown to influence the foraging and flight behaviour of bats. For example, Hecker and Brigham (1999) observed changes in flight altitude of forest bats in British Columbia, and related this to changes in the lunar cycle altering the distribution of insect prey. These behavioural responses to moon phases may have influenced the activity levels recorded in this study. Extending the study to survey sites on the same nights would enable such potential affects to be addressed. Assessing the two light treatments, compared to the dark control, in relation to insect abundance at each site would also be an important addition to any future study of this type. This would enable analysis of insect

attraction to light type and bat response to prey accumulations more directly than using bat passes and feeding buzz counts alone.

This experiment was limited by its scale it terms of replication (numbers of sites and nights) and perhaps the amount of, or height of lighting. Although sites where chosen by their good habitat quality and proximity to known roosts, bat activity was relatively low during the three-hour sampling period. However, the results highlight the potential of undertaking a similar study at a much wider scale incorporating more lighting (greater light spill along the linear feature and over the ground) for longer periods and greater replication (nights and sites) to overcome the high variability in bat activity. Whilst the lamps were adapted to create a UV component to the spectrum and a filter was incorporated, the two resulting spectra may not have been sufficiently different from each other or contain enough UV to adequately simulate conventional metal halide street lighting with sufficient intensity. Lux readings for the lights used in this experiment appeared to be sufficiently intense to be comparable to metal halide lights, however, the readings were taken at a distance of 5m in a narrow dark corridor where reflection from hard surfaces may have given unrealistic readings compared to on-site readings in the field, directly below the lights. Nevertheless, the localised intensity would appear to be comparable, if not brighter, than metal halide lux readings recorded 1.5m from the ground below street lamps (Stone et al., 2015). Perhaps the area of the overall light spill was insufficient and the duration of the experiment too short to observe any affects on bat activity, also a conclusion made in the study by Stone et al., (2015). Further work would be improved by using conventional lighting systems and using additional layers of UV filter. However, to power such lights would require the use of generators, creating further disturbance (noise) and additional costs.

Lighting technologies are likely to continue to improve at a faster rate than the ongoing replacement of old technology street lighting. It is therefore important that the effects on wildlife of the improved lighting technology for human application, are assessed before implementation on a wide scale.

Chapter 4

4. General Discussion

As the global human population grows, so too does its encroachment into dark landscapes with increasing levels of light pollution (Hölker et al., 2010). It is imperative that we increase our understanding of the ecological implications of light pollution so that developments can be made to improve technologies to reduce the impacts to wildlife. Artificial light has been shown to have a range of effects to a wide range of taxa, from small invertebrates to larger vertebrates, and the relationships between predator and prey interactions (Rich and Longcore, 2006).

This thesis has investigated the effects of artificial lighting on bats at a broad landscape scale and attempted to measure how intensity and wavelength differences affect the activity of commuting and foraging bats. The first experiment clearly showed that artificial light is detrimental to the activity levels of horseshoe species bats. Evidence was also found that the activity levels of the most common species of bat in the UK, the common pipistrelle, did not differ significantly different between light and dark locations, and in fact this species foraged more within a dark environment. Horseshoe spp. bats are specialists in terms of their call structure and wing morphology, which determines their preference for clutter based and edge habitat foraging. They may in effect, be hard wired by nature to be light averse (Russo et al., 2007), and the results of this investigation confirm theories about their ecology and habitat preferences and highlight the impending consequences of an increasingly artificial landscape. Pipistrelle spp. bats in the UK are considered to be generalists, comparable to corvids in the avian world, and so to discover that they also show a preference for dark environments was quite surprising given the number of researchers that have reported pipistrelle spp. foraging around streetlights (Rydell, 1992; Blake et al., 1994; Tomassini et al., 2014), as well as extensive personal observations and anecdotal evidence. Further investigations into habitat,

invertebrate densities, invertebrate composition and the amount of feeding by bats would be required to more fully understand environmental preferences and the impact of artificial light on bats. Previous investigations have not recorded activity at both light and dark locations simultaneously, and personal observations are more easily made next to a streetlight than in the dark. Chapter two of this study has provided evidence that dark environments are preferable to a common and widespread species of bat in the UK. Further evidence of the implications of light pollution will aid conservationists in convincing policy makers that light pollution needs to be addressed at a landscape scale not just in localised areas such as roosting sites for light averse species.

Previous studies have critically examined the effects of different lighting technologies on bat activity. This study has developed some of these ideas by examining specific differences in wavelength and accessing responses in bat activity. The second investigation in this thesis aimed to test how altering the light spectrum of lamps, specifically, reducing the amount of UV spectrum, might impact upon the activity patterns of bats. The UV component of artificial light spectra has been identified in several studies as an important contributor to changes in behaviour for various invertebrates and this study attempted to identify behavioural responses in bats. Whilst the experiment lacked in replication and scale and results did not show a significant change of activity between treatments, it has perhaps highlighted the potential for further investigations and the ease in which UV light can be filtered from standard metal halide lamps. It is widely accepted that light, and in particular UV light, negatively affects the behaviour of many invertebrate species (Frank, 1988; 2006), and this has higher trophic level effects, particularly for nocturnal predators of insects such as bats (Minnaar et al., 2015). For light averse bat species this has a

compounding effect whereby prey items can be attracted to artificial light and into a 'no go' area. The UV filtering of the experimental lights did not affect the wider spectrum and little overall intensity loss was incurred. Filtration in artificial streetlights may benefit both insect and bat communities whilst still retaining the colour rendering qualities of broad spectrum lighting preferred for human vision.

With greater understanding of light and its effect on wildlife we may be able to tailor light spectra to its application. Human vision is so well adapted to diurnal life, that we cannot implement a lifestyle at night without artificial light. For nocturnal animals, who thrive in darkness as well as we do in light, this is problematic. At present, little concern for wildlife is given to the technological improvements to illuminate our surroundings. The lighting technology market is driven, quite rightly, by energy efficiency but also by the requirement to produce colour rendering properties associated with human vision (Davies et al., 2013; Minnaar et al., 2015). For good colour rendering, artificial light must have a wide spectrum of wavelengths to replicate the full spectrum of the sun. Bats have been shown to have a relatively low threshold for photic entrainment altering their circadian activity rhythms (Erkert, 2004). Although there is limited literature on the spectral significance of light on photic entrainment, it is likely that full spectrum light has the most effect and perhaps the UV content is a significant component. In any case, artificial light exposure over extended periods can cause entrainment of the circadian clock resulting in potential problems with breeding, growth, foraging and communication over a wide range of species (Navara and Nelson, 2007; Rich and Longcore, 2006).

The lighting industry is a consumer driven market and rarely does conservation concern have an effect on the final product (Minnaar et al., 2015). Lighting technologies have improved over the decades to widen the spectrum while

reducing energy consumption (e.g. LPS updated to HPS). Broad spectrum artificial light is predicted to have a disparity of effects across taxonomic groups (Davies et al., 2013) due to differences in response to different parts of the spectrum. The latest LED technologies have spectra which can be directly controlled for a variety of applications. Experimental work is ongoing into the behavioural responses to different colour LED technology over a range of taxa (Spoelstra et al., 2015) with initial results showing that there is no 'one colour fits all' approach across taxa. This would imply that technologies should be installed in a case by case basis where possible. However, this is unlikely to be practical, since distributions of different taxa naturally overlap and what may be beneficial, or least disturbing to one taxon, can be the opposite to another. It may be ineffective to attempt to develop lighting technologies that are ecologically unbiased across all wildlife as well as acceptable for consumers. In short, developing lighting technologies and spectrum manipulations holds little promise and should not be considered a priority conservation measure (Minnaar et al., 2015).

We should discourage the use of more lighting as a result of an inevitable reduction in operating costs associated with energy efficient technological improvements; ultimately, cheaper light may result in more light and as developing countries grow economically, the problem could further accelerate. A more effective resolution to the impacts on wildlife and energy consumption is perhaps the implementation of intelligent lighting; where lights are activated by instantaneous requirement at source and which turn off when not required (Kyba et al., 2014). In addition to intelligent lighting, legislation to limit the intensity of installed lighting would prevent a more artificially illuminated environment as a result of the lower operating costs of newer technologies (Kyba et al., 2014). Continued satellite

monitoring of light pollution and light intensity on a global scale will help identify the remaining dark refuges for wildlife. Scientists and conservationists will be able to measure the effects of advances in lighting technology and changes in economic growth across the world on the extent of light pollution. With continued satellite monitoring of artificial light combined with growing evidence of the problems encountered by wildlife, such as those presented here, pressure can be mounted on policy makers to establish and expand dark refugia to enable wildlife to thrive in naturally light and dark conditions (Minnaar et al., 2015). In short, we need to reduce the amount of artificial light and the amount of time it is on for.

Appendix

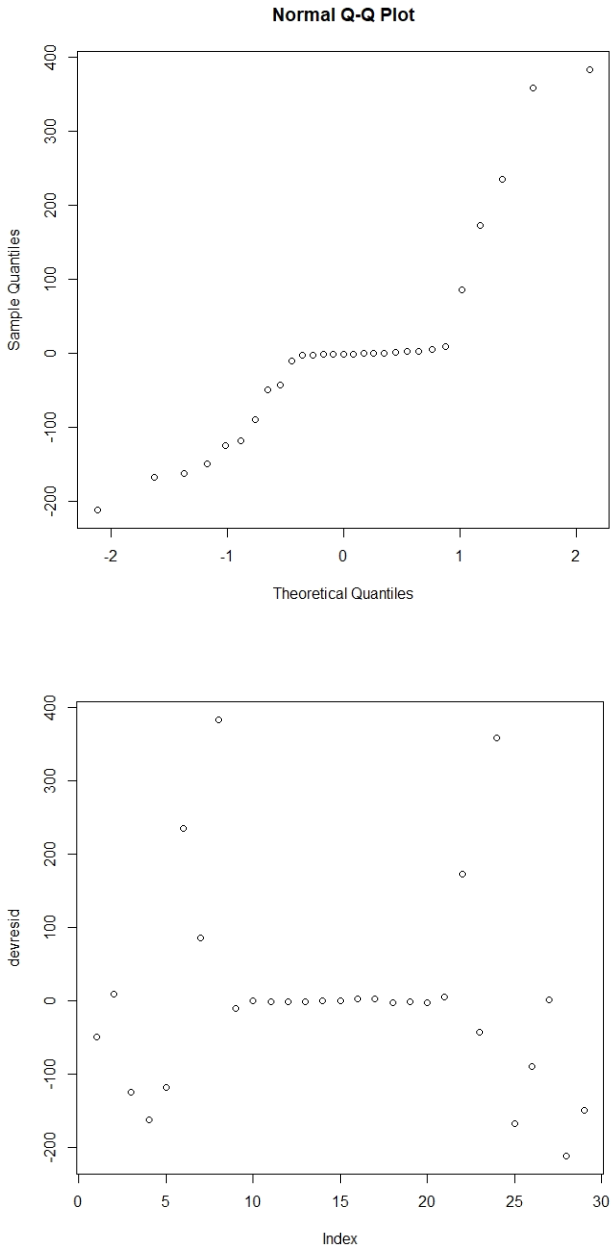

Figure 1. Residual plots of generalized linear mixed models showing non-normal residuals and hence justifying use of non-parametric statistics

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